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Effect of Artificial Lights on Sea Turtle Hatchlings orientation

MASTER'S THESIS

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Declaration

I hereby declare that I have done this thesis entitled Effect of Artificial Lights on Sea Turtle Hatchlings orientation independently, all texts in this thesis are original, and all the sources have been quoted and acknowledged by means of complete references and according to Citation rules of the FTA.

In Prague 22.4.2022
Bc. Tereza Znachorová

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Abstract

The topic of the thesis was the effect of artificial lighting on the orientation of hatchling sea turtles. The subject of the research study was to obtain data that would lead to a description of the behaviour of hatchlings in relation to artificial lighting. This thesis aimed to clarify sea turtle biology and evaluate the probability of disorientation of hatchlings concerning artificial lighting present nearby.

The thesis first focused on describing the biology of sea turtles (Chelonioidae). In the introduction, physiological features and morphological characters were generally described. Furthermore, the thesis focused on nesting and reproductive behaviour and also on possible threats to the species. In the next section, the taxonomy of sea turtles was described, focusing on the issue of one particular species - the green sea turtle.

The following part of the thesis was directed to the main topic: the threat to green sea turtle hatchlings by artificial lighting. The possible threats and endangerments of green sea turtles were mentioned. In addition to the general threats due to trade and industrial development, the thesis described the issue of artificial lighting near nesting beaches. It specifically dealt with the effect of artificial lighting on the behaviour of hatchling sea turtles. The possible disorientation of hatchlings became the subject of research for this thesis.

The research part of the thesis was carried out in collaboration with a Sea Turtle Conservancy organization. The study site was Tortuguero beach on the northern Caribbean coast of Costa Rica, in the province of Limón. This beach has black sand and is approximately 29 km long and is one of the most preferred locations by nesting females. For data collection, it was necessary to obtain hatchlings, which were gently collected from the nests and transferred to the laboratory of STC. The experiment was then conducted at night, the study site being a 1.2 km long section of beach bordered on one side by vegetation and the other by the sea. Hatchlings were released in a total of 26 circular arenas, repeated at different distances from the town. The necessary data were collected for the next part of the thesis by consistently observing the young in their seafinding ability. The data were then evaluated to determine the dispersion and disorientation.

The results of the research showed an effect of artificial lighting that was not so significant. Despite the illuminated town, most of the hatchlings decided to go in the right direction towards the sea, only in some cases in the presence of artificial lighting they decided to follow it. Despite the fact that a minority were affected by the artificial lights, these findings can be applied to local conservation activities that seek to limit the intensity of light smog through local ordinances and regulations.

Key words: Green sea turtle, Chelonia mydas, sea turtles biology, light pollution, disorientation, nesting biology, marine biology, vision, Tortuguero, Costa Rica

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List of the abbreviations used in the thesis

CCL: Curved carapace length

CITES: Convention on International Trade in Endangered Species of Flora and

Fauna

CMS: Conservation of Migratory Species of Wild Animals

DPS: distinct population segments

ESA: Endangered Species Act

IAC: Inter-American Convention for the Protection and Conservation of Sea

Turtles

IUCN: International Union for Conservation of Nature

MOU: Memorandum of Understanding

NMFS: National Marine Fisheries Service

SCL: Straight carapace length

STC: Sea Turtle Conservancy

USFWS: U.S. Fish and Wildlife Service

1. Introduction and Literature Review

The issue of sea turtle conservation has been largely overlooked in the past. Due to the development of society and unsustainable human behaviour, this species has become very endangered. Many turtles have died pointlessly, and entire populations have begun to decline. The conservation of sea turtles and animals, in general, should always be a current topic. That is why I have focused my work on specifying possible threats and their possible elimination.

The topic of my thesis is: "Effect of Artificial Lights on Sea Turtle Hatchlings orientation". The basis for my thesis was the literature of available authors, cited at the end of the thesis. The researchers of older authors, whose results have been followed up by new researchers, can be considered very useful. The issue of sea turtles has been discussed in the past by the authors Berkson (1967), Hailman and Elowson (1992), Jagger and Muntz (1993), Musick and Limpus (1997). Other colleagues have been very influential in the later period. The works of Wyneken et al. (2013), Wallace et al. (2005), Lorne and Salmon (2007), and others are considered to be very important studies of sea turtles.

The occurrence of sea turtles is dated to 220 million years ago, approximately 110 million years ago separate the species of sea turtles from terrestrial turtles. Unfortunately, due to the impact of civilization, the overall population of sea turtles has declined significantly and continues to face many threats. Despite this, the sea turtle has retained much of its range, focusing on food-rich waters as well as migratory areas to nesting beaches. In general, sea turtles are found in tropical and subtropical oceans around the world (Hirth 1997).

Morphological features may vary among sea turtle species, but several characteristics are common. A streamlined shell and wing-like limbs adapted for swimming are typical of all species. Because of the individual diet, each species has an adapted skull and jaws. Unlike terrestrial and aquatic turtles, the head and flippers of sea turtles do not retract into the shell. In reproduction and nesting, the sea turtle exhibits several interesting anomalies. Each female is capable of returning from long distances to the same nesting beaches during the reproductive season and can produce several clutches of eggs during the nesting season (Miller 1997). For nesting, the sea turtles

prefer a beach with certain characteristics but usually return to the same locations. Females try to minimize risks, for example, choosing a beach away from lighting, with a high shore to protect from being flooded by the tide. Each turtle lays 60-200 eggs in a single clutch, with the number varying from species to species (Shigenaka et al. 2021).

Once hatchlings hatch from their eggs, several circumstances affect their journey to the sea. There are many risks, one serious threat is light smog near the nesting beaches. After emergence, hatchlings become disoriented by artificial lighting on beaches and in nearby towns. Instead of heading for the ocean, they follow artificial light or wander in circles. Very often they die of exhaustion or dehydration before they reach the water (Humber et al. 2011).

The importance of this topic can also be seen in the obtaining of specialized knowledge related to this species. Sufficient awareness of the threats to sea turtles could lead to a deepening of interest in this species and its conservation.

1.1. Biology of sea turtles

Turtles (*Testudines*) are large air-breathing reptiles that inhabit tropical and subtropical seas around the world. Their weight ranges from 30 to 500 kg. Turtles differ from other reptiles in that their bodies are protected by a shell. The shell can be used to date the period of their life on land, with the oldest known members belonging to the Cretaceous period. This means they lived more than 220 million years ago. Sea turtles (*Chelonioidae*) split off from freshwater turtles about 100 million years ago. Research has shown that turtles are one of the oldest groups. They are an ancient group of animals, older than snakes and crocodiles, according to findings in the fossil record (Shigenaka et al. 2021).

Sea turtles are distinguished from terrestrial and freshwater turtles primarily by salt glands hidden in the skull, limbs transformed into flippers, and a distinct carapace. The shell is better adapted for movement in the sea. Their aerodynamic bodies and large fins are adapted to live in the sea. Sea turtles do not have teeth, but their jaws are modified into a beak, which they use to obtain food. Their ears are not visible, and their eardrums are covered with skin. They hear well, preferably at low frequencies. Their sense of smell is excellent. Interestingly, they can only see well underwater and are

myopic out of water. Despite spending most of their lives in the sea, they have strong attachments to land as will be discussed in later chapters (Arulmoorthy & Srinivasan 2019).

Due to their diversity, currently, living representatives of sea turtles are divided into seven species belonging to two families (Figure 1). One of the families is Dermochelyidae with only one species of leatherback sea turtle (*Dermochelys coriacea*). The second family Cheloniidae is represented by six species, namely the flatback sea turtle (*Natator depressus*), the green sea turtle (*Chelonia midas*), the hawksbill sea turtle (*Eretmochelys imbricata*), the loggerhead sea turtle (*Caretta caretta*), the Kemp's ridley sea turtle (*Lepidochelys kempii*) and the olive ridley sea turtle (*Lepidochelys olivacea*) (Shigenaka et al. 2021). A more detailed description of the species will be given in the chapter dealing with taxonomy.

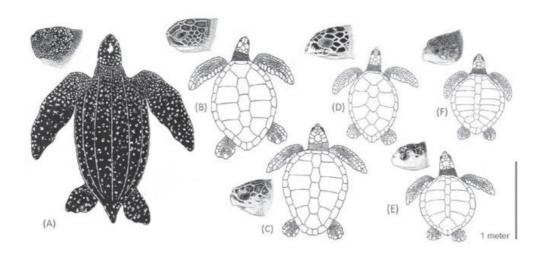


Figure 1. Sea turtle species found in U.S. waters to scale by average adult size (Thomas McFarland).

They are migratory creatures, so they are found in large geographical areas. They live in most oceans, but their home is most often the southwestern Indian Ocean, where five of the seven species are found (Musick & Limpus 1997; Plotkin 2003).

Despite the diversity of species, all sea turtles share certain characteristics. They are known for their ability to return to their birthplace unless they stay there directly. Another common characteristic is limited reproductive interactions. This causes a lack of gene transfer that would lead to the existence of separate breeding populations within

each species. This fact is another reason why sea turtles need to be protected (Wallace et al. 2010).

Most authors of the available literature commonly consider sea turtles to be tropical animals. In the opinion of other researchers, this interpretation needs to be a little bit modified. Turtles are not only found in warm waters. Loggerhead sea turtle species have nesting sites in subtropical areas. Other species of green sea turtles and loggerheads hibernate in cooler waters (Sale et al. 2006).

Leatherback sea turtles swim far, as far as the waters of the northern and southern hemispheres. The area around New England has recently been identified as critical habitat for the Atlantic ridley sea turtle and other species. Research shows that sea turtles are not only found in tropical areas but can survive in widely varying seawater temperatures. By studying their behaviour about temperature differences, there are further opportunities to characterize individual species. It is possible to know and understand the life cycles of each species. Tropical areas have minimal temperature fluctuation, and this has a significant impact on the reproductive biology and behaviour of turtles. The temperature has been shown to affect sex ratio, incubation period, turtle emergence from the nest, activity, and growth. Tropical environments also affect survival, hibernation, nesting interval, and distribution. Temperature is very important for sea turtles and their life cycle. The positive effects of a warm tropical climate have already been demonstrated in several existing studies. However, it is not the only important factor that can affect sea turtles (Bradshaw et al. 2007).

Sea turtles use two areas during their lives. One is the areas where they forage and nest, which are not very rich in food. The other foraging areas are where food is in contrast abundant. Between these habitats, thousands of kilometres apart, turtles migrate repeatedly. Because of the demanding migration associated with many threats, sea turtles do not breed regularly every year. However, when reproductive migration does occur, individuals meet and mate near the beaches where the females hatched. A female can lay as many as seven clutches, each containing 80-100 eggs, in a reproductive season lasting less than three months. After about 60 days, the young hatch. As with many reptiles, the sex of the young is determined by the temperature during incubation. Higher temperatures produce females and lower temperatures produce males. The hatchlings need to get to the sea as quickly as possible and use visual orientation to do

so - they tend to leave dark areas and head for the starlit water surface. During their slow growth, sea turtles undergo dramatic ontogenetic changes. From an initial oceanic juvenile stage, they usually recruit into inhabitants of nearshore habitats when they reach a certain size, where they mature over the next few years and from there travel to hatching areas to reproduce. However, little is known about the biology of sea turtles between the time they first enter the sea and reach sexual maturity (Plotkin 2003).

The sea turtle life cycle (Figure 2) usually begins in a tropical country when the female sea turtle lays her eggs on the nesting beach. This varies from species to species, but after six weeks to two months, hatchlings emerge and try to dig their way to the surface. The baby turtles then crawl as fast as they can to the sea and if they manage to get into the water they swim toward the open sea.

The hatchlings first swim into the open ocean, where they stay for quite a long time, which can take decades. This period is often called "THE LOST YEARS" because the movements of turtles during this phase are very difficult to track and their behaviour is impossible to define. After these lost years, sea turtles grow to about the size of a dinner plate. Their stay in the open ocean and as juveniles, they return to coastal waters to forage for food and mature. During this period, turtles are highly mobile and forage over large areas of the ocean depending on species and food availability (Rusli 2019).

Sea turtles gradually mature and after ten to fifty years of the hatchling stage, they reach sexual maturity and are able to mate. Sexual maturity is individual depending on the species. Once turtles reach adulthood, they migrate from the developmental area to the mating area. Females come ashore to lay their eggs, usually where they were hatched. Males migrate from the mating area to feeding grounds each year. Unfortunately, sea turtles have a very low natural survival rate and are at high risk. Approximately only 1 in 1000 turtles reaches the adult stage. A single female turtle can mate with multiple males and a single clutch of eggs can have up to five fathers. These interesting reproductive capabilities are due to the ability of females to store sperm in the fallopian tube until ovulation (Phillips et al. 2013).

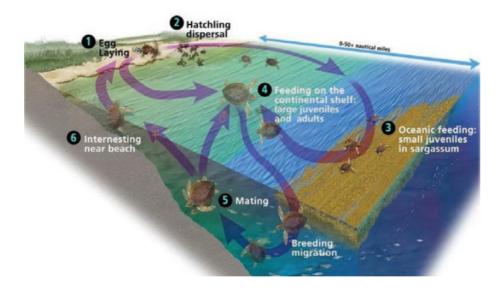


Figure 2. The life cycle of sea turtles (Kate Sweeney).

1.1.1. Physiology and behaviour of sea turtles

The research work of the authors cited above has shown that most turtles can be described as more a surface swimmer, as they do not dive to extreme depths. Most of them stay at depths of up to 200 meters, where they forage for food, mat,e or sometimes even sleep. Considering that sea turtles use their lungs to breathe and depend on air, this behaviour is admirable. They breathe in by raising their heads above the surface and between dives, they essentially live off that breath (Polovina et al. 2003; Sale et al. 2006).

Although most sea turtles reside in the upper 200 m of the water column, leatherback turtles have been recorded diving too much greater depths, up to 1280 m. As the turtle descends to depth, it experiences increasing hydrostatic pressure at a rate of 1 atm for every 10 m of depth (Doyle et al. 2008). As the pressure increases, the pressure force acts on all the gases in the body. When animals exhale before diving, such as whales, this is not a problem. Sea turtles, on the other hand, inhale a lot and if the pressures between the air in their lungs and the surrounding water do not equalize, this can cause significant structural damage to the thoracic region. However, the lungs of sea turtles are capable of handling this situation. They are protected during collapse at depth so that damage does not occur, and there is no detachment of the visceral and parietal pleura (Berkson 1967). This leads to minimal pressure differences. When the lungs collapse, they expel all the compressed air into the trachea. This protects the body

of turtles by reducing the possibility of gases diffusing into the blood. On the contrary, if gases were exchanged between the respiratory tract and the bloodstream under high hydrostatic pressure, serious problems could occur. Nitrogen anaesthesia could occur on the descent of the turtle to depth and conversely, decompression sickness could occur on the ascent (Davenport et al. 2009).

Other authors report that sea turtles are among the most active air-breathing marine vertebrates, spending only 3 to 6 % of their time at the surface. While most sea turtle species do not normally dive deeper than 10 to 50 m, leatherbacks have been recorded diving much deeper. The deepest reach is over 1,000 meters. The situation is influenced by many factors such as natural conditions and the environment. Normal dives can last around 15 minutes to almost an hour or more. During normal dives, sea turtle emerges to take a good breath before running out of oxygen. After raising its head above the surface, the sea turtle exhales strongly and quickly and takes several breaths. It requires only a few breaths, each less than a few seconds, to empty and fill the lungs. Such high airflow rates are possible because turtles have large, thickened airways and their lungs are widely divided. This increases the exchange of gases between the lungs and the bloodstream. When diving, the heart rate slows and blood flow to organs and muscles is altered to control oxygen use and maintain function. This respiration is necessary for sea turtle survival, but it also has major disadvantages. Sea turtles become vulnerable to threats at the sea surface when they emerge, including floating oil and possible chemicals in the air (Shigenaka et al. 2021).

Situations that are uncomfortable and dangerous for sea turtles can occur. Sometimes sea turtles are forcibly held underwater, for example, due to entrapment in artificial materials such as thick oil. In this case, they quickly use up their oxygen stores and convert glucose to lactic acid for energy. This process is called anaerobic metabolism. Lactic acid levels can rise rapidly, even to lethal levels. Although there are physiological mechanisms that compensate for these effects, recovery can take many hours or even days. These are very stressful events for sea turtles, especially when they last for a very long time or are too intense. During recovery, there are additional risks as turtles are vulnerable to predators and other threats (Hart et al. 2010).

The properties of their cardiovascular and respiratory systems allow them to dive and control buoyancy. Due to their constantly salty diet, they also have modified lacrimal glands through which they expel excessive salt. These physiological characteristics mean that sea turtles are well adapted to deep diving. Another important feature is their ability to remain underwater for extended periods. Wintering turtles have a record number of hours underwater. They can remain submerged for more than seven hours between breaths (Hochscheid et al. 2005). When turtles are not hibernating the dive time is much shorter, they do not remain underwater without breathing for more than 60 minutes (Hatase et al. 2007).

The ability to dive for a longer period means that sea turtles have other adaptations in their respiratory and cardiovascular systems. The following abilities are considered the most important. The first is respiratory tidal volumes in sea turtles, with a capacity of 1 to 2 litres of inhaled oxygen per breath. This is important during diving because of the rapid uptake of oxygen and scavenging of carbon dioxide (Lutcavage et al. 1990). The second anomaly required for life is oxygen management at great depth. Although sea turtles breathe before diving, their lungs collapse at great depths. Oxygen inhaled before diving is only available during shallow dives. To dive deep, turtles can store large amounts of oxygen by attaching it to respiratory pigments such as haemoglobin and myoglobin. This stored oxygen remains available to them at greater depths. A third ability of sea turtles when diving is to divert blood flow from nonessential organs while maintaining blood flow to the heart, brain, central nervous system, and kidneys. The absence of blood in non-essential organs helps reduce the rate of oxygen consumption and increases the time a turtle can dive in for one breath. As a result of these amazing abilities, sea turtles can spend long periods underwater without oxygen deprivation (Bradshaw et al. 2007).

The food and drink, that turtles need to live to contain large amounts of seawater. The concentration of salt is excessively high, up to three times that of vertebrate cytoplasm. For most animals, this extremely high salt intake is lethal; their cells dehydrate and die. Sea turtles have to cope with this situation by using their nephrons. Nephrons are found in the kidneys of reptiles, but they have short loops of Henle that are unable to fully remove this excessive salt from the blood. In marine reptiles, it is different, they have accessory salt glands. These modified glands can secrete a hyper-saline solution twice as concentrated as seawater, and therefore six times more concentrated than typical vertebrate cytoplasm (Reina et al. 2002).

The research studies of authors have confirmed the admirable travelling abilities of sea turtles. They are capable of migrating over vast distances and travelling large numbers of kilometres between breeding and foraging areas. Since they can cover thousands of kilometres, they move over a wide range of latitudes. The migration range of some species includes tropical and temperate waters. They are predisposed to this behaviour due to their excellent navigational abilities. Sea turtles orient themselves according to the magnetic field of Earth and other environmental impulses, which allow them to return predictably to specific areas to feed and breed (Phillips et al. 2013).

The life cycle of sea turtles includes several phases that together span decades. At each life stage, turtles may be found in several different habitat types. Each habitat represents a particular vulnerability to anthropogenic threats. These life cycles vary greatly depending on geographic location, both within and between species, and even between individuals within populations. U.S. beaches and waters provide habitat for six of the seven species of sea turtles, but occurrence varies by life stage and species (Shigenaka et al. 2021).

The food and feeding of sea turtles depend on the area where they are found. Sea turtles are omnivorous. Their food includes representatives of the marine plant and animal kingdoms, such as jellyfish, sponges, small crustaceans, and small fish. Research has shown that the gut microbiota of sea turtles and the genetic mapping of their microbiome likely co-shaped their evolution over tens of millions of years (Davenport et al. 2009). In their early life, turtles referred to as hatchlings or juveniles live near the sea surface where they swim. They get carried away by the current and eat anything on the surface. Due to oceanographic forces and wind, oil accumulates in the same places where the turtles are found. Small turtles are not yet smart enough to get out of the oil, especially the tougher form. Oil spills are one of the serious threats to sea turtles (Ackerman 1997).

The diet of sea turtles varies from species to species, and also at different life stages. Their diet is diverse, ranging from bottom-dwelling animals and vegetation to invertebrates and seaweeds found on the sea surface. The turtles are in danger while feeding. A major risk can be non-natural materials moving in the sea. Sea turtles use multiple senses to find their prey, but even this does not always protect them. Despite these abilities, they are unfortunately capable of ingesting foreign material, including forms of oil such as tarballs. The turtle mistakes foreign materials for food and is not

always able to distinguish them. At all life stages, most turtle species forage for food on the sea bottom, where they may accidentally ingest sediments and any chemicals or other substances in those sediments. Two species, loggerheads and Kemp's ridleys, are known to dig into the seafloor in pursuit of invertebrate prey (Shigenaka et al. 2021).

The marine ecosystem is a functioning and meaningful environment. Sea turtles play a very important role here. For example, the authors highlight their vital role in the functioning of coral ecosystems. Hawksbill sea turtles, whose main diet consists of marine sponges (*Cnidaria*), regulate the growth of fungi on coral reefs. In doing so, they directly influence the composition, structure, and species diversity of these ecosystems (Davenport et al. 2009).

1.1.2. Nesting biology

Research on sea turtles mating, and nesting has provided a wealth of interesting information. Much of the research has focused on female nesting and hatchling emergence from the nest. The advantage of collecting the data needed for the studies was that nests with hatchlings could be found relatively easily and then studied.

Because of the threat to sea turtles, one of their important abilities is high reproduction. Each female is capable of producing several clutches during the nesting season (Miller 1997). During the mating season, competition and fierce fighting take place between males, usually with several males attempting to mate with one female at a time. The research work of the authors mentioned above has shown that sea turtles are monogamous, polyandrous, and polygynous. After fertilization, sea turtles undergo egg maturation, where the foetus is produced. The foetal eggs are protected by protective membranes that allow full embryonic development. However, the foetal eggs need an airy environment to incubate, so the female must emerge from the water. They deposit their eggs in nests on tropical or subtropical beaches (Phillips et al. 2013). Sea turtle egg development is a lengthy process that begins a year or more before eggs are laid on nesting beaches. The female forms a yolk sac that it nourishes over many months. During this time, the females feed well and accumulate the energy resources necessary for reproduction (Brothers & Lohmann 2018).

After reaching the nesting beach, the females have already formed the yolk necessary for all the egg-laying that will take place that year. The eggs are formed in the female reproductive tract, including the formation of the outer shell. The developing embryo at this stage is microscopic and consists of a tiny collection of cells. The length of the incubation process is temperature dependent. In general, higher incubation temperatures will reduce the time to hatching (Jong et al. 2009). However, too high a temperature is a major threat to sea turtle foetuses. Temperatures higher than 33 to 35 °C can cause poor quality and impaired locomotion of hatchlings trying to escape from nests (Segura & Cajade 2010). Research has confirmed that the behaviour of turtles that have built nests in shade or open areas will result in changes in the phenotype and performance of the individual (Rusli 2019).

Nesting does not occur very often, with an interval of two to four years between nesting seasons (Chaloupka 2001; Sims et al. 2008). Mating of turtles takes place near the area where the female then lays its eggs. This is usually the area around beaches, but mating can also occur during the migration or on fishing grounds. However, this behaviour is very rare, as studies have shown. Fertilization occurs inside the body and turtles can store sperm for a long time after mating. During mating, male sea turtles use the claws on their front flippers to attach themselves to the carapace of female (Miller 1997).

They return to lay the eggs at the place of birth, sometimes even to the same beach. The females crawl the beach to nest above the high tide line. This may be due to the high weight of the turtle (60 - 600 kg) causing great resistance to movement. People may find the movement of turtles along the beach energetically demanding and very exhausting. Therefore, sea turtles shorten their distance from the shore to the nesting site during high tide. During nesting, the turtle often sheds tears, thereby ridding the body of excess salt in the blood (Lutz et al. 2002). For nesting, the turtle chooses a beach with certain characteristics. The beach needs to be high enough to avoid being flooded with seawater at high tide, and it needs to have sand that allows for gas exchange. The sand must be moist and fine enough so that it does not collapse when the turtle excavates the egg chamber. Sea turtles lay 60-200 eggs in each clutch. Each species lays a different number of eggs. The unique features of the tracks left by the

turtles are used to identify the nest on the beach. These tracks can be used to identify different species (Hays et al. 2010).

Sea turtle nesting is typically at night, the night-time helps the turtles avoid dehydration from the long strenuous crawl from the water to the beach and back (Talbert et al. 1980). Exceptions are Kemp's ridley and Flatback sea turtles. During high tide, the female sea turtle emerges from the water onto the beach and begins the overall nesting process. The female will first find a suitable site that is above the high tide line. The female synchronously moves her left and right flippers back and forth, throwing away sand and slowly lowering her body, starting to lower her centre of gravity until she is below beach level. The behaviour of the female throwing sand away while excavating the nest is called "body pitting". She also uses her hind flippers to help her get deep enough. The size of the hind flippers greatly influences the depth of the nest chambers. The hind flippers act as shovels to scoop sand out of the nest cavity, the larger they are the larger the cavity. At the same time, it moves its hind flippers left and right. This behaviour is known as "egg chambering" (Rusli 2019). The turtle tries to dig as deep a hole as possible, digging as far as it can reach. In leatherback turtles, the hole can be up to 80 cm deep (Shigenaka et al. 2021). The shape of the nesting chamber resembles the shape of a bulb (Figure 3), this is in order to keep the temperature even between all eggs during incubation. Individual species have a nest chamber shape tied to maternal morphology and performance during reproduction (Segura & Cajade 2010). If female sea turtles find an obstruction such as roots, dead coral, or gravel while excavating a nest they will abort their work. They will move to another location and begin body pitting again or may also go back out to sea and start digging the nest the next night (Rusli 2019).

When the female turtle is satisfied with the nest construction and considers it complete, she lays her eggs through the oviduct by dropping two or three into the nest at a time. Little by little it lays about 100 eggs. Based on research, it is believed that when the eggs at the top touch the tail of female, it is a sign to the turtle that the nest chamber is adequately full. However, other researchers, Hailman and Elowson (1992), disagree. They believe that this feedback is not the only clue to the completion of egg-laying. According to their findings, some turtles stop laying eggs earlier. The whole process takes about 10 minutes depending on the species. When the turtle finishes laying eggs,

it covers the nest cavity with its hind flippers and rests like this for a relatively short period, about 5 minutes. This short time can be used by scientists and conservation teams to safely measure morphological characteristics and attach identification tags. After this brief pause, the turtle begins work on camouflaging the nest. Using her front flippers, she scatters sand over the covered egg chamber and gradually moves forward several metres. This behaviour is designed to confuse predators by creating an elongated pile of sand on top of the original nest chamber to symbolize a false nest. When the turtle is satisfied with the camouflage of the nest, it immediately returns to the sea and the offspring receive no further parental care (Rusli 2019). During a nesting season, a female sea turtle may nest between 1 and 14 times. Within this range, the reproductive output of some sea turtle species can be more than 1,000 eggs in a single nesting season (Shigenaka et al. 2021). The time it takes for a turtle to crawl to the beach to dig a nest, lay eggs and return can take 2 to 4 hours (Sims et al. 2008).

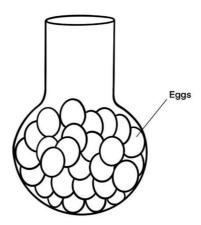


Figure 3. Illustration of a typical shape of a nest chamber with eggs (Tereza Znachorová, 2022).

Unfortunately, unsuccessful nesting attempts also occur. Researchers recognize this by the tracks left on beaches that show only crawling, not nesting. This phenomenon is known as "false crawling" (Talbert et al. 1980). During nesting, female sea turtles are quite sensitive to any disturbance on the nesting beaches. This may be one reason. They do not like to be disturbed and avoid human presence and noise, some predators, or lighting from nearby cities and tourist areas. They will often abort their nesting attempts or even abandon nesting if the disturbance is continuous (Phillips et al. 2013).

After nesting, sea turtles migrate to locations that may be thousands of kilometres away (Shillinger et al. 2008). Here they accumulate the necessary energy reserves for nesting the following season. Because of the energy costs of migration and nesting, it can take many years for individual female sea turtles to acquire the necessary resources (Wallace et al. 2005). Male turtles are slightly better off. They also make similar migrations to female turtles, but they do not have to produce eggs. Thus, the energetic costs of reproduction are lower for males and thus male turtles may return to their breeding grounds more regularly than female turtles (Hays et al. 2010).

Nesting is typically seasonal, lasting 2 to 6 months per year. For this period, turtles need privacy, so nesting is most often solitary and individuals nest independently. Exceptions may be kemp's ridley and olive ridley turtles, which nest in dense aggregations called arribadas. During an arribada, up to thousands of individual females may nest on a single beach for 3 to 10 consecutive days.

Other authors also describe the nesting characteristics of those turtles as different from other sea turtles in many ways. Both species nest during the day and individual females often nests every year. Both ridley species also nest singly or in synchronized mass nesting events arribadas. Arribadas usually occur in groups of three to four-week intervals and can include hundreds or thousands of females (Shigenaka et al. 2021).

Some studies by available authors suggest that the reason for this long hiatus may be due to the long cruises of sea turtles in the open ocean. This period probably cannot be accelerated, because the turtles are foraging and migrating from one place to another in search of food. When the nesting season occurs, the turtle stays near the beach where it lays its eggs for quite a long time (Hart et al. 2010).

Meanwhile, in the nest with the laid eggs, further development gradually occurs, causing the embryo and surrounding membranes to attach to the top of the egg. This period is very sensitive to external disturbance of the nest. Any movement of the egg, such as accidental digging or other disturbance, can kill the embryo. During incubation, the eggs take in air and water from the surrounding sand. Chemicals in the sand can also be absorbed by the embryo and change the gas and fluid exchange properties of the shell. Also, changes in the colour or composition of the sand can affect the temperature or physical properties of the nest and significantly alter the incubation environment (Tuxbury & Salmon 2005).

The incubation period of hatchlings lasts about two months, all influenced by the ambient temperature (Shigenaka et al. 2021). The sex of sea turtle hatchlings is influenced by temperature; incubation temperatures during the middle trimester determine the sex of the embryos. Females are produced at higher temperatures and males are produced at lower temperatures. The temperature at which an equal percentage of males and females are produced is usually referred to as the key temperature, which ranges from 28 to 31 °C (Ackerman 1997). Studies have not yet revealed the exact genetic mechanism that causes sex differentiation, but it is likely to be associated with the Lhx9 gene (Bieser et al. 2013). Temperature also significantly affects the percentage of eggs in each nest that successfully hatch and leave the nest. As an example, when nest temperature exceeds 36 °C or drops below 24 °C for an extended period, fatal threats to developing embryos occur (Ackerman 1997). Hatchlings burrow to the surface more or less simultaneously. Most hatchlings emerge from a single nest in a single night and are followed on subsequent nights by a few stragglers. The night is good for hatching because the high temperatures of the surface sand can hinder the movement of the young. It is important to keep the sand cool, so daytime emergence on cloudy days or after rain is possible. When the hatchlings first emerge from the eggs, they weigh only about 25-45 g, depending on the species (Shigenaka et al. 2021).

Sea turtle hatchlings generally hatch collectively in individual nests, as the movements of individual hatchlings encourage neighbouring turtles to also break free from the eggs. Although no studies by published authors have provided concrete evidence of the importance of vocalization between eggs, it may be very important for hatching. Some other reptiles, such as freshwater turtles and crocodiles, synchronize their hatching through vocalizations (Ferrera et al. 2013).

After hatching, the young dig up to the surface of the sand, a journey that can take 2 to 3 days. The temperature of the surface environment can affect the process of the hatchlings emerging from the nest. During the day, they become immobile if encounter hot sand. During the night, when it cools down, the hatchlings will start moving again. On the surface of the beach, they crawl quickly to the brightest horizon. On dark, unlit beaches, it's usually the ocean, illuminated by reflected light from the moon and stars. The hatchlings move away from the darkness of the beach dunes and move towards the brilliance of the surf. The ideal situation is in the wild in lonely

places. On beaches near cities, artificial lights visible from the beach can lead to the poor orientation of hatchlings. These become a natural clue for finding the sea, hindering their ability to find the right way (Tuxbury & Salmon 2005).

The authors describe how hatchling and female sea turtles have poor vision and rely on the weak light of the horizon and the darkness of the land to find the ocean. Sea turtles evolved long before man created artificial lights and modified beaches. Lighting on beaches, buildings, vehicles and other sources disorients turtles and prevents them from finding their way to the ocean. This can result in death. Even remains of human activity on beaches, such as tire ruts and other created depressions in the sand, can create insurmountable physical barriers for hatchlings. It is a natural process for hatchlings to reach the water, the sea, and the ocean, rather than artificial light (Shigenaka et al. 2021). Hatchlings that find the ocean leave their nesting beaches and swim away from the coast to reach the open ocean. Usually a distance of 200 metres. They swim continuously for almost the entire first day, in a period called "frenzy" (Wyneken & Salmon 1992). The name is derived from the behaviour of the juveniles, which swim very vigorously to get out of shallow, predator-rich waters as quickly as possible. They never return here until they reach sexual maturity (Rusli 2019).

Over the next week, swimming activity gradually decreases as the juveniles get further and further out to sea (Wyneken & Salmon 1992). As the juveniles get further from land, they drift away by the tides of the open ocean. They will join other planktonic animals and spend many years drifting in these currents (Arthur et al. 2008). The exact movements of the hatchlings during this period are not yet mapped, and scientists do not yet know how long the hatchlings will spend in the open sea. It is thought they spend their earliest and most vulnerable years swimming in the sea in giant patches of seagrass. Their only activity seems to be to swim, eat and grow. Once the turtles reach a certain size, they appear at feeding sites in coastal waters. At this age, turtles remain associated with surface habitats as ocean juveniles. Examples include the Sargassum seaweed in the Atlantic and Gulf of Mexico (Hart et al. 2010).

As they grow to larger body sizes, they move closer to shore as neritic juveniles. They grow slowly and take 15 to 50 years to reach reproductive maturity, depending on the species. There is no way to determine the exact age of a sea turtle from its physical appearance. All sea turtle species need to spend at least ten years in the ocean to reach

maturity, but sometimes this time is much longer. For example, some species, such as green turtles and loggerheads, can take more than 30 years to reach adulthood. Some species can live for more than 100 years (Arulmoorthy & Srinivasan 2019).

The open ocean environment contains fewer predators than coastal areas, making this area safer for the development of juvenile sea turtles. For these reasons, sea turtle nesting behaviour may be influenced by female searching locations for their nests where coastal currents easily carry hatchlings away from the beach and out into open water (Putman et al. 2010). When juvenile turtles are approximately the size of a dinner plate, their typical behaviour is manifested by migration to tropical or subtropical coastal habitats (Berube et al. 2012). Young turtles remain in these areas until adulthood when they begin their reproductive migration. When a turtle leaves a foraging site, the journey to the reproductive areas can exceed 1000 km. Sea turtles tend to return to the beaches on which they hatched when searching for suitable nesting sites (Lohmann et al. 2008).

Migration has also been described by other authors whose research has shown how sea turtles migrate across the open ocean to their home range as adults for breeding. Adult male turtles return to foraging areas after mating, while adult females remain during the mating season, which can last 1-2 months. After eggs are laid in nests on the sandy beaches, new hatchlings emerge, and the cycle continues again (Shigenaka et al. 2021).

Studies in recent decades have revealed another amazing ability of sea turtles. Turtles are able to navigate using the magnetic field of Earth. This ability, along with the use of olfactory cues and chemical imprinting from natal beaches, may account for their native homing ability. Research suggests that biogenic magnetite crystals provide sea turtles with the ability to sense the magnetic field. However, this assumption has not yet been confirmed (Irwin & Lohmann 2005).

1.1.3. Morphology

Most researchers describe certain common morphological features typical of all sea turtle species. The main ones are the flattened, aerodynamic shell and the winged limbs adapted for swimming. The skull and jaws of each species are adapted to their specific diet. Unlike terrestrial and aquatic turtles, the head and flippers of sea turtles cannot be pulled into the shell (Shigenaka et al. 2021).

Other authors have also described the large, aerodynamic shells that characterize various species of sea turtles. Research has shown that each sea turtle species has several distinguishing features, these are used for identification. Different species have different numbers of prefrontal scales, the small, paired scales found above the nostrils and between the eyes. An important distinguishing tool is the carapace of turtles, which may also have varying numbers of plates arranged in a unique pattern. Depending on the species, the adult shell varies in shape from oval to heart shaped. In all species except leatherbacks, the bony shell consists of enlarged conjoined ribs, and the spine is attached to the carapace. The ventral side of the shell is called the plastron. In all species except leatherbacks, the shell is covered with a layer of horny plates called scute. Scutes are firm but flexible, not fragile. Scientists can identify sea turtle species by the number and pattern of scute (Figure 4). The further subdivision is possible according to the labels. These are between the eyes (prefrontal scutes), running through the centre of the carapace (vertebral scutes), adjacent to the vertebral scutes (lateral scutes) and connecting the plastron to the carapace (inframarginal scutes). The leatherback turtle has a thick, oily skin that is an excellent insulator and allows this species to venture into cold water. The carapace of the leatherback consists mostly of cartilage raised inconspicuous longitudinal ridges. The large bony shell of the sea turtle protects from predation and abrasion (Tuxbury & Salmon 2005).

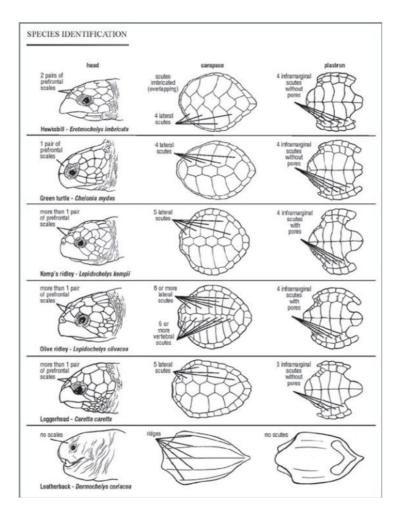


Figure 4. Guide for identification of species. Prefrontal scales are located between the eyes. Lateral scutes lie on each side of the vertebral scutes (Dawn Witherington and Janette Wyneken).

Another typical common feature of sea turtles is the distinctive toothless beak at the front of the skull. It develops from hard bone or cartilage and is covered with horny keratin. Sea turtles of all species have no openings in the temporal region of the skull behind the eye socket, meaning they are anapsids. Studies originally assumed that anapsids were a monophyletic group. However, recent research has shown a change. The anapsid skull of turtles may be due to reversion from diapsid ancestors and not from direct descent. This discovery means that sea turtles may be more closely related to lizards and snakes than to birds and crocodiles (Lyson et al. 2010).

There are also noticeable differences between sea turtle species. A distinct morphological difference between sea turtles and other Testudines is evident in the shape of their limbs. Terrestrial Testudines have robust limbs that are short and occasionally have swimming membranes. In sea turtles, on the other hand, the limbs are

broadly flattened and form large paddle-shaped flippers. The structure of the hind limbs is provided by greatly elongated toes. The front ones show a short, thick radius and ulna. Both the hind and forelimbs are very important in the movement of turtles in seawater. The front flippers are used by turtles to move through the water using a lifting propulsion system. There is a noticeable similarity that is analogous to bird wings (Renous et al. 2000). The hind flippers are much shorter than the front flippers and function as a rudder for steering in the water. Sea turtles are very efficient swimmers and possess the larger musculature needed for swimming. Therefore, unlike other testudines, they are unable to retract their limbs or necks into their shells (Shigenaka et al. 2021).

Sea turtles are relatively small in size and weight after birth. They are usually less than 10 centimetres in length and weigh around 55 grams. The growth rate of baby turtles is rapid, and it is incredible that they eventually grow up to be some of the largest reptiles on the planet. They reach sexual maturity at different times between the ages of 7 and 40 years (Chaloupka & Musick 1997).

During sexual maturity, sea turtles devote most of their available energy to reproduction. As a result, the growth rate slows down to the point of being almost irrelevant. There can be great variability in the size of adult turtles. The largest sea turtle of all existing species is the leatherback. At maturity, the leatherback turtle can measure over 1.4 m in curved carapace length (CCL) and weigh between 200 and 1000 kg. On the other hand, the smallest of the sea turtles is the Ridley, but even these can grow to larger sizes, up to 80 cm (CCL) and weigh up to 50 kg (Price et al. 2004).

1.1.4. Taxonomy and sea turtle species

Sea turtles belong to the order Testudines, along with other aquatic and terrestrial turtles. Sea turtles form the only species that diverged from other turtles during the early Cretaceous period (Hirayama 1998). Research studies by the authors have shown that at least three families evolved from the original lineage of sea turtles: the Protostegidae, Cheloniidae, and Dermochelyidae (Kear & Lee 2006).

Only two families of sea turtles can be found in the world's ocean waters today: the Cheloniidae and Dermochelyidae. The family Cheloniidae is characterized by a "hard shell" and its evolution has been dated to 60 million years ago. Cheloniidae contains six extant species within five genera: the flatback turtle (*Natator depressus*), the green turtle (*Chelonia midas*), the hawksbill turtle (*Eretmochelys imbricata*), the loggerhead turtle (*Caretta caretta*), the Kemp's ridley turtle (*Lepidochelys kempii*) and the olive ridley turtle (*Lepidochelys olivacea*). Members of the "soft-shelled" Dermochelyidae family evolved about 90 million years ago and contain the only extant species within a single genus: the leatherback turtle (*Dermochelys coriacea*) (Duchene et al. 2012).

Other authors provide a similar division, listing two families - Dermochelyiidae with one representative leatherback and Cheloniidae with six species. The family Cheloniidae is characterised by keratinous plates covering a well-developed bony carapace. In contrast, the great leatherback has a carapace consisting of a thin, tough layer of elastic skin that is reinforced by thousands of small bony plates. This is probably due to deep dives for food and possible compression. The leatherback is the deepest diving reptile (Lyson et al. 2010).

Sea turtles live mainly in tropical seas, where breeding sites may vary by species. The green turtle breeds in the tropics and the more common loggerhead turtle also lays eggs in the Mediterranean. However, the largest range, not only of the sea turtle group but also of all reptiles, is that of the leatherback, which inhabits all the world's oceans. Leatherbacks lay eggs in the tropics and subtropics and their feeding habitats can be observed in northern areas above 50°N. Other researchers divide individual sea turtles into species based on certain morphological features. These are mainly the shape of their head and shell, also the number and pattern of their plates and scutes. Further subdivisions are made according to the overall size of the sea turtle and the colour of its body and shell. Like their colleagues, the authors define seven basic species and several others with a lesser representation of turtles. Five species can be commonly recorded in U.S. waters and a sixth species, the olive ridley turtle, occurs in U.S. territorial waters. Occurrences of a seventh species, the flatback turtle, have been recorded only near Australia and Indonesia. All species are divided into different populations or subpopulations based on their separate geographic areas and degree of genetic relationship (Shigenaka et al. 2021

The Genus Caretta: Caretta caretta (Linnaeus 1759): the Loggerhead Turtle

The specie of sea turtle that is distinguished from the others mainly by its shape is the Loggerhead turtle. These turtles have dark brown to maroon shells and yellow plastrons (Figure 5). They are named Loggerhead because they have the largest head and jaw relative to the body size of all sea turtles. Adult loggerhead turtles are between 70 and 110 cm in SCL and weigh between 60 and 200 kg (Lohmann et al. 2008).



Figure 5. Loggerhead sea turtle (*Caretta Caretta*) (Matty Testoni, 2021).

Their diet is very varied, and they are not picky. Loggerheads are the most omnivorous of all sea turtles. Their large head and strong beak allow them to eat many hard-shelled invertebrates such as molluscs and crabs. Their diet may also include tubeworms, sea pens, fish, algae, whip corals, sea anemones, barnacles and shrimp.

Just as their diet is varied, their habitats seem to be quite diverse. Loggerheads live between deeper continental shelf areas and shallow estuaries and lagoons. Important loggerhead turtle nesting sites are found on the east and west coasts of the United States, east and west Africa, the eastern Mediterranean, east Asia, and Australia. Loggerhead turtle nests in the most temperate zone of all sea turtles (Paladino & Robinson 2013).

Studies of migratory behaviour have shown remarkable findings. Loggerhead turtles perform one of the longest migrations in the animal kingdom. Turtles hatched on Japanese beaches swim across the North Pacific Gyre to places along the Mexican coast where the coastline is rich in food for young turtles. After reaching sexual maturity, these turtles migrate back across the Pacific Ocean to return to their nesting beaches in Japan. They travel an astonishing 10,000 kilometres on their migration (Nichols et al. 2000).

The Genus Chelonia: Chelonia mydas (Linnaeus 1758) the Green Turtle

The genus Chelonia contains only one extant species: the green turtle, which is characterised by its unique shell shape and its typical colour (Figure 6). The colouration of the skin and shell is predominantly green or brown to black. This has led some researchers to divide the green turtle into two separate species or races: the green turtle (*Chelonia mydas mydas*) and the East Pacific green turtle or black turtle (*Chelonia mydas agassizii*). However, molecular studies have shown that both green and black turtles are, at least genetically, the same species (Kear & Lee 2006).

The black turtle is characterized by the dark black colour of its shell and plastron in adulthood. The posterior shell is more concave in black turtles and more convex in green turtles. Both species have one pair of prefrontal scutes with four pairs of coastal scutes. Adult green turtles reach 80 to 120 cm in straight shell length (SCL) and weigh 65 to 200 kg. Black turtles tend to be smaller at 65 and 90 cm SCL and weigh between 50 and 150 kg (Paladino & Robinson 2013).



Figure 6. Green sea turtle (*Chelonia mydas*) (Nathan Cook, 2022).

The food that turtles eat is the same for both species, both are herbivorous. Green turtles consume seagrasses and marine plants of the genera *Zostera*, *Thallassina*, *Enhaus*, *Posidonia* and *Halodule*. Black turtles, on the other hand, most often feed on red algae. However, recent studies by the authors have shown that this species can also supplement its diet with gelatinous prey (Amorocho & Reina 2007).

Green turtle habitats are in shallow tropical waters. They are seasonal visitors in more temperate areas. Important nesting sites for green turtles are found along the Atlantic and Pacific coasts of Central America, Hawaii, islands in West Africa, Ascension Island, the islands of Malaysia, and the islands of northern Australia. There is also a range in another area, the eastern Mediterranean, which also has a small and relatively endangered population of green turtles (Arthur et al. 2007).

This species is further discussed in more detail in a separate chapter, as the green sea turtle became the focus of research for this thesis.

The Genus Lepidochelys: *Lepidochelys kempii* (Garman 1880) the Kemp's Ridley Turtle, *Lepidochelys olivacea* (Eschsholtz 1829) the Olive Ridley Turtle

Another sea turtle species studied is the genus Lepidochelys, which consists of two species, the Kemp's ridley (Figure 7) and the olive ridley turtles (Figure 8). Interesting findings by the researchers are that the Kemp's ridley is the rarest sea turtle, while the other type of turtle, the olive ridley turtle, is the most abundant. Studies have shown that these two species were artificially isolated with the closure of the Isthmus of Panama about 14 million years ago. A similar situation, which also led to the isolation of the Kemp's ridley turtle, also occurred in the Gulf of Mexico (Irwin & Lohmann 2005).

Again, the shape and colouration of the shell are considered distinctive and obvious at first glance. However, the colour of the shell is not prominent. Kemp's and olive ridleys have a dull olive-coloured shell and yellow-white plastrons. The shells are highly arched and are generally as wide as they are long. Anatomically this genus of sea turtles is the smallest and adults of both species reach between 50-80 cm at SCL and weigh between 30 and 50 kg. Unlike the previous Chelonia species, Kemp's ridley turtles are carnivores. Their most important food is mainly swimming crustaceans and

molluscs. Olive ridley turtles are omnivorous and have a more diverse diet that consists of salps (*Mettcalfina spp.*), algae, jellyfish, fish, benthic invertebrates, molluscs, crustaceans, and bryozoans.



Figure 7. Kemp's ridley sea turtle (Lepidochelys kempii) (Blanca Zapata, 2021).



Figure 8. Olive ridley sea turtle (*Lepidochelys olivacea*) (Karla Barrientos-Muñoz).

When it comes to nesting, these turtles are exceptional in their behaviour and can be solitary or in large arribada groups. The largest arribadas are found in Orissa, India, and more than 100,000 olive ridley turtles have been recorded in this location in a single night. This high nesting density means that many turtles are digging up eggs that were laid the previous night. This creates a large number of rotting eggs, which

provides fertile conditions for bacterial growth. This situation means that the bacteria struggle with the reduced oxygen concentration in the sand, raising temperatures and infecting and killing many of the eggs. As a result, the hatching success of arribada nests is greatly reduced. Unfortunately, it is often only between 1 % and 10 % (Valverde et al. 2010).

The occurrence of these turtles can be seen in the warm waters of predominantly tropical areas. Kemp's ridley turtles are found in shallow waters in the Gulf of Mexico. During the summer months, hatchlings will also visit estuaries along the east coast of the United States. Two major and important nesting sites for Kemp's ridley turtles have been defined. These are Rancho Nuevo, Mexico and South Padre Island, USA. Each species prefers a different location. Arribadas are found only at Rancho Nuevo and Olive ridley turtles are found in warm pelagic waters in the Atlantic, eastern Pacific and the northern Indian Ocean. Significant breeding grounds for Olive Ridley turtles are found on the Pacific coast of Central America, West Africa, the East Indies, and the tropical Atlantic coast of South America (Lohmann et al. 2008).

Through research and observations of turtles, in the 1950s, the scientific community first discovered Kemp's ridley arribadas occurring at Rancho Nuevo. It was only shortly thereafter it was discovered that this population was, unfortunately, declining rapidly. The reasons for the decline were attributed to extensive egg collection by poachers and predators. Also, a large number of adult Kemp's ridleys died in nets during shrimping in the Gulf of Mexico. To protect the species, the Mexican government quickly enacted a law, and the U.S. banned the importation of shrimp harvested in a way that would endanger the lives of turtles. Kemp's ridley is still very far below its historical population curve, but the situation is beginning to improve. Researchers believe that Kemp's ridley is now recovering (Paladino & Robinson 2013).

The Genus Eretmochelys: *Eretmochelys imbricata* (Linnaeus 1766), the Hawksbill Turtle

Another species of turtle, the hawksbill turtle gets its name from its narrow and elongated jaw. Its shape is remarkably similar to the beak of a raptor (Figure 9). The hawksbill turtle's body and shell colouration are quite distinctive. The hawksbill's carapace is mottled black, brown and yellow, while the plastron is a bright yellow to

beige. The size of adult hawksbill turtles is highly variable. Carapace length ranges from 50-90 cm at SCL and weight is between 40 and 80 kg at maturity (Paladino & Robinson 2013).

The shape of the beak, which is very sharp, is perfectly adapted to feeding on sponges. Hawksbill turtles are one of the few spongivorous animals and electron micrographs of their gastrointestinal tract have shown micrococci with millions of quartz spicules embedded in the tissue. Their food mainly includes tunicates, sea anemone, bryozoans, molluscs and marine plants which are important components of the diet of these turtles (Price et al. 2004).

Hawksbill turtles are very fond of warmth and are therefore generally found in tropical coral areas, on reefs with shallow water. Important turtle nesting sites are found in the Caribbean, equatorial Brazil, Southeast Asia and the western Indian Ocean. Small populations of hawksbills have also recently been discovered in the eastern Pacific Ocean. Research has found interesting information that these hawksbills from the eastern Pacific Ocean are more commonly found in association with mangroves than with coral reefs (Gaos et al. 2010).

The threat to hawksbill turtles has historically been quite high, and they have been subjected to intense hunting around the world due to the beauty of their shells. The use of the shell as a manufacturing material was historically used primarily to make items from "tortoiseshell". These were mainly eyeglass frames and hairbrushes, which were made from tortoiseshell. Unfortunately, various Hawksbill souvenirs can still be found for sale in many parts of the world. In Asian countries, prepared adults and their shells were prized as symbols of longevity. Currently, all legislation and laws to protect sea turtles should put an end to this activity (Paladino & Robinson 2013).



Figure 9. Hawksbill sea turtle (*Eretmochelys imbricata*) focusing on the beak (Kerry Lewis, 2021).

The Genus Natator: Natator depressus (Garman 1880) the Flatback Turtle

On the other hand, another species of Flatback turtle is not very distinctive in colouration or shape. Flatback turtles have a low arched carapace with an inverted rim at the rear of the animal. The colour of the carapace is dull olive-grey, and the plastron is light cream (Figure 10). The shell scutes of flatback turtles are oily and relatively thin. There is not much variation in the size and weight of adult turtles, flatback turtles are between 80 and 100 cm in CCL and weigh between 60 and 100 kg. Flatback turtles also have no problems with food; they are omnivores and consume a wide variety of mostly soft prey including seagrasses, molluscs, jellyfish, crabs, shrimp, fish, soft corals, and sea cucumbers (Nichols et al. 2000).

They live in only a few localities and have very limited distribution. It is found only in shallow, sheltered coastal waters off northern Australia and the Gulf of Carpentaria. Significant breeding grounds are similarly found along the northern coast of Australia. The flatback turtle is unique in that it is the only sea turtle that does not live free in the open ocean during its juvenile life (Walker & Parmenter 1990).

Their nesting sites are so remote that a thorough population assessment has not yet been possible for this species. Nevertheless, studies have shown that many of the breeding sites for this species are located near large oil production or refining facilities. The risk of nesting turtle populations from this industrial production is great. This issue is currently of great concern (Paladino & Robinson 2013).



Figure 10. Flatback sea turtle (*Natator depressus*) (iNaturalist, 2021).

The Genus Dermochelys: *Dermochelys coriacea* (Vandelli 1761) the Leatherback Turtle

Due to its size, the Leatherback turtle can be considered the dominant species. These sea turtles are the largest and most visually distinctive of all sea turtle species. They do not have the characteristic "hard shell" of the Cheloniidae instead, their shell consists of cartilaginous osteoderms under a layer of leathery skin. Seven cartilaginous spines extend along the anteroposterior axis of the leatherback shell, which facilitates the laminar flow of water over the turtle's body, thereby reducing drag. The colouration of leatherbacks is also distinctive, being black or dark blue with white spots and white plastron (Figure 11). The size and weight of these turtles are significant, at maturity, they range from 130-190 cm at CCL and can weigh between 200 and 1000 kg (Lohmann et al. 2008).

Leatherbacks are obligate carnivores and feed only on soft gelatinous invertebrates such as flagellates, cnidarians, ctenophores and salps. The upper beak of their mouths even has two sabre-like projections. These bite through the air bladders of swimming stingrays and colonial jellyfish. Leatherback turtles primarily inhabit open marine waters populated by plankton. Their foraging movements often target aggregations of prey. These are typically found along with dynamic oceanographic features such as fronts and upwelling zones that lead to large aggregations of food (Shillinger et al. 2008).

The migratory patterns of leatherback turtles can be likened to long-term stays in large feeding areas that can encompass entire ocean basins. Significant breeding grounds are found on the Pacific and Atlantic sides of Central America, Papua, East and West Africa, Sri Lanka and Guyana. Adult leatherback turtles have the largest range of any reptile. Research has confirmed a very interesting fact. This species of turtle has been found in water temperatures of 7-10 °C while maintaining a body temperature above 20 °C (Lyson et al. 2010). This ability to adapt is called gigantothermy and allows turtles to maintain their body temperature even in cold waters. Their large, round body shape, thick layer of fat and counter-current heat exchange in their circulatory system serve this purpose. Leatherback turtles also use a high level of activity to generate heat from their muscles (Paladino et al. 1990).



Figure 11. Leatherback sea turtle (*Dermochelys coriacea*) (iNaturalist, 2015).

1.1.5. Survival rate and threats

Sea turtles are known in their history for frequent movement from place to place, as well as their longevity. For these reasons, various risks and anthropogenic threats have occurred at each stage of their life history. These circumstances have led to the conservation dependence of all sea turtle species (Wallace et al. 2010).

One of the most serious threats is the expanding industry; currently, human behaviour is not always environmentally friendly. As marine reptiles, sea turtles feed on food in the sea. Their biology may pose a risk to them. For example, all sea turtles must swim to the surface to breathe, rest and feed. This behaviour is necessary for life but is a risk wherever oil is extracted, or shipping takes place in the ocean. Sea turtles and their hatchlings on land are equally exposed. The behaviour of turtles coming ashore to lay their eggs puts them, their eggs and hatchlings at risk of exposure to oil and beach spill response (Shigenaka et al. 2021).

Populations of all seven sea turtle species are in steep decline. Four of the seven species are considered critically endangered, and the other three are considered threatened with extinction. The relatively best situation is in the Atlantic Ocean, where they have been protected for some time, especially on beaches. There are organisations involved in their conservation. The situation is worse in the Pacific Ocean, where the population curve is falling steeply. The worst is the negative development in the Indian Ocean. Here, entire populations of sea turtles have already gone completely extinct in many places (Paladino & Robinson 2013).

The different types of risks and other threats are closely related to the life cycle of turtles. The terrestrial phase, which is relatively short in the life of sea turtles, is the worst time for threats to turtles. During this time, females, eggs and hatchlings are exposed to many snares. The clutch of the eggs is highly vulnerable, either through prolonged flooding of the clutch by tides, predation or even intraspecific destruction. Many of the dangers are natural and common in nature. Unfortunately, however, human activity is fundamentally affecting their intensity, and this can be fatal to sea turtle populations. Thanks to global climate change, sea levels are rising, threatening to flood eggs more frequently. Another concern is human-introduced predators such as dogs and rats. Due to coastal development, natural beaches are shrinking, and nesting space is decreasing. It is more common for a turtle to physically destroy a previously deposited

clutch in the same place while digging its nest. Residual light entering the beach from urbanised areas disorientates hatchlings. Recreational and tourist areas near beaches play a large role in the ability of hatchlings to find the sea. However, the biggest and worst problem in many places remains the direct collection of turtle eggs and the killing of females for meat (Rusli 2019).

In addition to terrestrial areas, turtles are also endangered in marine and ocean waters. Adult sea turtles in the ocean are almost devoid of natural enemies, yet they are highly threatened by human activities. A major problem for them is intensive fishing, where they can get caught in nets. Another risk is the increasing pollution of the seas, not only with plastics but also with chemicals. Turtles are at risk of lifelong diseases, which they are more easily susceptible to due to the weakened immunity caused by marine pollution.

Immediately after birth, the hatchlings are exposed to many risks from all sides. Due to the high mortality rate of newly hatched young, sea turtles have developed a life strategy. Mortality is compensated by high reproductive potential and longevity. We know that each turtle can have several clutches per year and that some species reach old age. This strategy has worked for millions of years, yet today sea turtle populations are in decline. Unfortunately, largely due to increased mortality from human activity (Spotila et al. 2000).

Sea turtle hatchling mortality is very high as described by the authors. During the early life stages, survival rates are lowest, and it is estimated that only one in a thousand hatchlings reach sexual maturity. The main risks include the laws of nature, with many sea turtle nests flooded by high tides, washed away by storms or overheated by high temperatures. Humans and animals are other risks. Hatchlings are collected by humans or hunted by native and introduced species such as dogs and raccoons. The hatchlings that survive and can successfully leave their nest must find the ocean. Unfortunately, this journey sometimes becomes deadly for them. Many hatchlings are attacked when they crawl into the water by crabs, birds, dogs, raccoons and varans. Other individuals become disoriented by artificial lighting on beaches and in nearby towns. Instead of going to the ocean, they follow the light and die of dehydration before they reach the water. Even young ones that make it to the ocean are not saved. Here they are at risk of predation by fish and birds, especially in coastal waters. As juveniles

progress towards open water, predation rates are thought to decline. Predation rates will continue to decrease as the turtle begins to grow and the protective shell becomes more rigid (Humber et al. 2011).

The risk of mortality in hatchlings decreases during the juvenile period. Adult sea turtles have few natural predators. Only on the beach at nesting time are they threatened by dogs, crocodiles and big cats. In the water, the situation is better, with adult turtles being preyed upon only by large sharks and killer whales. Unfortunately, humans also put turtles at risk. Sea turtle hunting still exists where in many parts of the world people continue to hunt adult sea turtles for their meat and shells (Humber et al. 2011). Another risk is the large commercial fishery where pelagic longline fishing and shrimp trawlers catch numerous sea turtles as bycatch. While the capture of sea turtles is mostly incidental, many individuals are injured or die as a result of swallowing hooks or becoming entangled in nets (Wallace et al. 2010).

With current climate change continuing to take place, there is growing concern about how sea turtles will be affected by this. Rising sea levels will reduce the amount of available nesting area for many populations. In addition, rising temperatures may lead to increasingly biased sex ratios in females due to temperature-dependent sex determination and reduced hatching success (Saba et al. 2012).

Despite all the threats, efforts to improve are visible. Many notable sea turtle recovery efforts are occurring. All sea turtles are currently listed on the Appendices of the Convention on International Trade in Endangered Species of Flora and Fauna (CITES). All species except the flatback turtle are also listed as threatened or endangered on the International Union for Conservation of Nature (IUCN) Red List (Lohmann et al. 2008).

Based on the described threats to sea turtles, legislation has been modified in their favour. The ESA-listed status of sea turtles was established. All sea turtles occurring in the U.S. are listed as endangered or threatened under the U.S. Endangered Species Act (ESA). The definition of endangered means that the species is in danger of extinction in the total or majority population. Threatened is defined as a species that is likely to become endangered in the near future. Kemp's ridleys and all populations of hawksbills and leatherbacks are listed as endangered under the ESA. Olive ridleys are listed as threatened, except for the breeding population in the Pacific Northwest of

Mexico, which is listed as endangered. Green turtles are listed as threatened wherever they occur in U.S. waters in the Atlantic, Gulf of Mexico, and the Caribbean, as well as in the eastern Pacific. Loggerheads in the Gulf of Mexico are part of the Northwest Atlantic population and are listed as threatened. Loggerhead turtles in the North Pacific are also listed as endangered (Rusli 2019).

Within a species, subgroups or populations may be designated as distinct population segments (DPS) under the ESA and may have a different status under the law. Critical habitats, which are areas necessary for the conservation of species listed under the ESA, has been designated under the ESA in the U.S. for green turtles, hawksbills, leatherbacks, and loggerheads (Shigenaka et al. 2021).

In addition, there are several international treaties and conservation agreements (e.g., Inter-American Convention for the Protection and Conservation of Sea Turtles (IAC), IUCN). A Red List of Threatened Species has also been established. This document reflects their status as a species considered at risk of extinction if current threats are not reduced. Of particular importance, the CITES includes all seven species of sea turtles in its Appendix I, which prohibits their operation in international trade.

Two other U.S. agencies, the National Marine Fisheries Service (NMFS) and the U.S. Fish and Wildlife Service (USFWS) share federal jurisdiction for sea turtle conservation and recovery. The roles of these two agencies are defined in a joint Memorandum of Understanding (MOU), originally executed in 1977 and updated in 2015. USFWS is responsible for legal protection in the terrestrial environment and NMFS is responsible for legal protection of turtles in the marine environment. In addition, state agencies coordinate with federal agencies to fulfil management responsibilities within their respective states (Shigenaka et al. 2021).

As can be seen, the threats to each sea turtle species are clearly defined. For example, green, leatherback and hawksbill sea turtles are classified as endangered under the Endangered Species Act in the United States, while loggerhead and olive ridley sea turtles are listed as threatened. Internationally, green and loggerhead sea turtles are listed as endangered species. This means that they face a very high risk of extinction in the wild shortly. By the International Union for Conservation of Nature and Natural Resources (IUCN), while hawksbill and Kemp's ridley sea turtles are listed as critically endangered species, Olive ridley sea turtles are listed as endangered and leatherback sea

turtles are listed as vulnerable species. This means that all listed species face an extremely high risk of extinction in the wild in the immediate future (Arulmoorthy & Srinivasan 2019).

1.2. Biology of Green Sea turtle

The green sea turtle (*Chelonia mydas*) is a species of large sea turtle in the family of the Cheloniidae. It was first described by researchers in 1758 as *Testudo mydas* and was subsequently placed in the genus Chelonia in 1800. Later research revealed the worldwide distribution of the green turtle, and the species came to be referred to as having several morphologically distinct forms. Currently, taxonomy distinguishes two possible subspecies- the green turtle (*Chelonia mydas*) and the black turtle (*Chelonia mydas agassizii*). For the purposes of this paper, the green sea turtle will be described (Witherington et al. 2006).

1.2.1. Distribution

Although the overall sea turtle population has already declined significantly and is highly endangered, the green sea turtle has retained much of its historical distribution. The range of this species includes waters rich in food resources, as well as areas with migratory routes in search of nesting beaches. In general, it has been recorded in tropical and subtropical oceans around the world (Figure 12) (Hirth 1997).

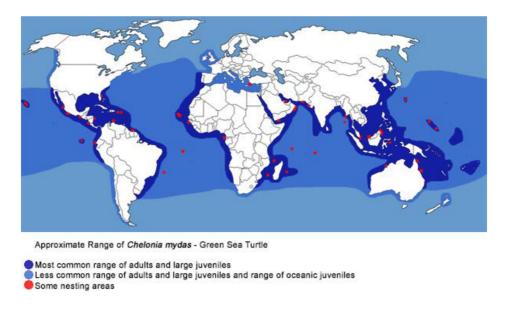


Figure 11. Worldwide distribution of green sea turtle (http://www.californiaherps.com/)

The lowest abundance is seen in the eastern and central Pacific and north-eastern Atlantic, and several breeding sites have unfortunately been extirpated. In contrast, the greatest abundance can be seen mostly on the eastern Pacific and Atlantic coasts, especially in coastal waters throughout Florida. The authors agree that approximately 99% of green sea turtles nest on Florida beaches. The largest nesting beaches in the Atlantic are thought to be those off Tortuguero, Costa Rica. In the Indian Ocean, the largest nesting sites are in Oman and the islands surrounding Madagascar and in the Indonesian region, but populations are declining significantly. In the Pacific Ocean, Raine Island in Queensland, Australia, is identified as the largest breeding site (Bjorndal et al. 2000).

Despite Florida's location near the northern boundary of the Atlantic green sea turtle nesting range, a large proportion of turtles nest on beaches. Florida is second in the ranking of beaches lining the western Atlantic Ocean in the number of nesting beaches, just behind Costa Rica. This may be due to the abundance of seagrass or algae, which are important food items for green sea turtles. During the winter, they feed in the lagoons and estuaries of the Mosquito Lagoon and Indian River Lagoon, on coastal Atlantic reefs, and seagrass beds in Florida Bay. In summer, turtle numbers also remain in these areas, but their foraging range extends as far north as Massachusetts and the Gulf of Mexico (Schmid 1998).

1.2.2. Morphology

Green sea turtles have a brownish coloured carapace with yellowish plastrons. The green colour designation in the name comes from the large, greenish fat found under the shell, not from outward appearance. The reasons for which these turtles once became famous were nutritional. Turtles were once commonly used as food, and the fat under the shell became the main ingredient in turtle soup. Green sea turtles reach the largest size among hard-shelled turtles alive today, with only the leatherback turtle being larger. The shape of the shell is broad and oval, with an average length of about 98 cm, generally ranging from 88 to 104 cm. Weight is also not insignificant, with adult females recorded between 104 and 177 kg (Witherington et al. 2006).

Another distinctive morphological feature that differentiates the green sea turtle from other species is the two large prefrontal scales between the eyes and the heavily serrated lower jaw. The contrasting colouration is very striking already in the hatchlings, which are contrastingly coloured. The ventral surface is creamy white and contrasts clearly with the dark carapace (Figure 13). The exception is the dark pigmentation in the distal half of the fins and the dorsal part. Early in juvenile life, patterns of ray-like stripes appear on the carapace and dorsal scales. The colouration of the carapace is more contrasting and striking in juvenile green sea turtles than in adulthood. Yellow, brown, green and black colours can be seen. However, colouration may vary between populations. In adult green sea turtles, the colouration of the shell is already faded, and the ray patterns are not as clear as in the juvenile stage. The colour is an olive shade with light and dark spots visible inside each scale. The lower part of the shell, which can be referred to as the abdominal region, also changes in colouration at different stages of the green sea turtle's life. In new-hatched coastal juveniles, the colour is a creamy yellow, later in the open ocean it lightens to white and in adulthood, the colour is a deep yellow (Hirth 1997).



Figure 13. Colouration of hatchling green sea turtle showing a dark carapace contrasting with the light colour of the ventral side (Tereza Znachorová, 2021).

The external appearance of males and females is identical at first sight. The adult male differs from the female by a thick prehensile tail and a strongly curved claw at the edge of each front fin. The claws of female are straight and shorter. Male green sea turtles are several centimetres shorter than females in terms of carapace length at maturity (Godley et al. 2002).

1.2.3. Reproduction and nesting biology

The mentioned authors were concerned with the monitoring of green sea turtles during the courtship and mating season. Studies have shown that green sea turtle interactions indicate promiscuous behaviour. As a result, multiple paternity often occurs in green sea turtles. Female choice is highly competitive with males so males will mount any object similar in shape and size to a female green sea turtle. Sexual act with a female requires some communication skills and even then, there is a risk of rejection. The male approaches the female cautiously and nips her neck and fins before the actual mounting manoeuvre. The female turns to face the male and her behaviour shows a clear refusal or acquiescence. The authors believe that a female that turns her belly in a vertical position toward the male is more likely to refuse copulation (Bjorndal et al. 2000).

Successful copulation is usually accomplished by the male approaching the female from behind and pressing his soft flexible abdomen against the female's shell. The male hooks the front edge of the female's carapace with the curved claws of the front flippers and grasps the hind edge of the carapace with the hallux claws of the hind flippers. The thick, prehensile tail curls under the female and in this position sexual contact can occur. The bifurcated spermatic duct of the penis allows the transport of sperm into each of the female's oviducts (Miller 1997). This coupling can last for several hours, and if there is a lot of competition between males, biting on the fins, tail and head can occur. This danger faces both mounted males and recalcitrant females. Copulation can often be visible because green sea turtles tend to mate at the surface near nesting beaches. However, this is not always the case; sometimes mating takes place at a courtship site that may be distant from the nesting beach (Hirth 1997).

The most common location with the greatest abundance of nesting beaches for green sea turtles is the coast of Costa Rica and Florida. The turtles nest mostly at night, on sandy beaches on the mainland coast, barrier islands, volcanic islands, and atolls. Research in this area has shown that they most often prefer beaches with rougher sand and prominent foredune. They also nest where there is minimal development and artificial lighting. Green sea turtles are very sensitive to any disturbance during the breeding season. Females that have privacy complete approximately half of their nesting attempts. If they are disturbed by humans before laying eggs, they rarely complete their

nesting attempt. Studies show that the successful nesting process for green sea turtles takes approximately two hours. Preparing the nesting site takes 40% of that time, laying eggs 13% of the time, and covering and camouflaging the nest 47% of the time (Witherington et al. 2006).

Green sea turtle breeding is seasonal, taking place in the summer months in the non-tropics and the tropics, it can take place in all four seasons, often peaking during the rainy season. Every two to four years, female turtles return to the same places and beaches where they were hatched. They usually nest several times during the breeding season. Fertilised females climb onto the nesting beaches by moving all their limbs at the same time. This activity leaves clear marks, given the weight and size of the turtle and the length of their flippers. The trail is approximately 120 cm wide, with visible markings from the hind and front flippers and a thin trail from the tail. The green sea turtle builds its nest using both front and hind flippers by burrowing into the sand. The appearance of the nesting site is determined by the nature of the substrate, its roughness and moisture content. If it encounters no obstacles, it will dig a 2m diameter pit. Once the nest is covered, the site can be recognized by an oval mound of 6 to 10 m (Hirth 1997).

The average frequency of clutches can be determined quite accurately; researchers have no problem finding nests visible by the features described earlier. Nevertheless, not all nests can be found, so data on the number of clutches may be rather underestimated. The studies concluded that the average nesting frequency ranged from 2 to 5.5 nests per season. The average number of eggs per clutch is very similar and ranges from 104 to 147 eggs. There is a slight increase in clutch size with age and also an increase in clutch frequency. However, it is not entirely clear how green sea turtle fertility changes throughout a lifetime, but the longest period of breeding recorded for females was 20 years. This repeated observation of nesting behaviour occurred in Tortuguero, Costa Rica, and confirmed the relatively long reproductive capability of the green sea turtle (Witherington et al. 2006).

After eggs are laid in the nest, a period of incubation occurs, the length of which is influenced by the temperature in the nest. On a temperate and sunny beach, it is between 52 and 56 days, on a rainy tropical beach in Costa Rica this period is around 60

to 65 days. In extreme cases, in rainy and cold weather, it can take up to 4 months for the hatchlings to emerge (Miller 1997).

The sex ratio of hatchlings depends on the temperature during incubation. Research has shown that at higher temperatures, mostly females hatch and at lower temperatures males hatch. The base temperature at which the sex ratio would be 1:1 is approximately 28.5 - 30.3 °C. Other circumstances such as geographical location or nest location may also influence sexing. Research has been done in Tortuguero, Costa Rica, where the hatchling ratio was estimated to be 67 % female during a dry, warm year (Spotila et al. 2000). Other authors have conducted research during a rainy and cooler years and estimated this ratio to be only 10 % females. These data show a large effect of temperature on sex formation during incubation (Witherington et al. 2006).

Immediately after the eggs hatch, hatchling sea turtles try to get out of their nests. One of the first migratory movements takes place already inside the nest at this time. Inside the nest, the hatchlings move in such a way that the sand falls out from under them. The aim of the young is to make a vertical movement approximately 40 to 70 cm long, outwards towards the surface. This is followed by a group movement upwards and a subsequent escape from the nest. Usually, this behaviour occurs at night or occasionally in rainy and cloudy weather. The low surface temperature of the sand motivates a group of young to emerge in mass. On hot days without rain, the emergence of hatchlings from the nest is minimal because the hot sand and high air temperature pose a danger to them. Movement from the nest towards the ocean is controlled by light signals; the young perceive the water surface as a wide and bright horizon and crawl in that direction (Witherington & Martin 2003). If a group of newly hatched hatchlings is oriented correctly, they will spend 5-10 minutes making their way to the sea. If they manage to get into the sea safely, they swim toward the open ocean where they feed on seagrasses and macroscopic algae. This first teamwork in a group of hatchlings, as they emerge from the nest together and run into the ocean, ends when they reach the water surface. Once they reach the open ocean, contact between the new hatchlings is very rare and completely random. Reunions only occur when they return to shallow coastal waters (Berry et al. 2013).

The survival rate of hatchlings is not clearly recorded. The authors mention the probability that approximately the same number of hatchlings that hatch in the nest will

reach the sea. But on naturally illuminated beaches! Artificial lighting disrupts their movements and draws them into the dunes and hazards. Lighting can cause up to 100% mortality of the entire nest. Another danger occurs in the sea, in the surf zone, where mortality caused by the fish can be high (Paladino & Robinson 2013).

Green sea turtles are exceptional among other turtles in their behaviour on land. They come ashore for reasons other than nesting. Also, to bask and rest in some places in the Pacific. They're the only species of turtle that has been recorded doing this. In some places in Hawaii and Galapagos, male and female green turtles come out of the water and stay on the beach for several hours a day. This unusual behaviour has been studied and the reason why these turtles do this has not been clearly defined. There are several hypotheses. It may be an escape from predators, or a need to increase body temperature by basking or destroying ectoparasites (Witherington et al. 2006).

Research focusing on mitochondrial DNA has revealed much important information. Relatedness between breeding groups is strongly influenced by the attraction of females to the natal beach. The ability of females to return to the same beach where they hatched is very dominant. Genetic similarity between turtles that share regional nesting beaches has also been shown. However, male green sea turtles do not return to specific nesting beaches. Genetic material passed by both males and females has shown that there is mediated gene flow between nesting groups but is limited by the distance between nesting sites, for example, the greatest genetic differences are between green sea turtle populations from the Atlantic-Mediterranean and Indo-Pacific regions (Spotila et al. 2000).

Yet there are many genetically distinct breeding populations in each of these oceanic regions. The western Atlantic with the wider Caribbean Sea area is the breeding ground for most green sea turtles. And it is here that the most pronounced genetic split between the two populations has been recorded. These are the north-western region-Florida/Mexico and Costa Rica and the south-eastern region- Isla Aves and Suriname. Each of the four breeding populations is genetically distinct (Brothers & Lohmann 2018).

1.2.4. Life Stages

After reaching the water surface, juvenile green sea turtles swim vigorously from land to the open ocean, where they search for food near the surface. The very active swimming pattern observed in these juveniles means that they can do whatever it takes to quickly disperse and avoid potential predators. Soon after hatching, they start feeding on plant and animal material. After a hectic journey, the hatchlings naturally get carried by the ocean currents throughout the ocean basins. Although relatively little data has been collected on turtle ecology at this life stage, there is evidence that juvenile turtles feed on organisms associated with convergence zones near the ocean surface. These include wind-dispersed plankton floating on the surface or food related to the genus. This period when hatchlings only swim and feed in the open ocean lasts until they grow to approximately 20-30 cm carapace length. Growth rates during the oceanic stage can only be speculated upon, as data collection during this period is difficult for researchers. Research has shown the validity of a 3-to-5-year period in the ocean environment before the green sea turtle returns to coastal waters. Here they settle, close to the mainland shores, islands and reefs, and feed on seagrasses and macroscopic algae in shallow coastal waters. Usually, no more than 10 metres deep, green sea turtles burrow into soft mud, rock ledges and coral growths to rest and avoid being carried away by the ocean currents. These foraging habitats are important to them, as are the migration corridors that extend along the reefs and across the open ocean. In the historical evolution of turtles, there have been known cases of local grazing competition between green sea turtles in areas rich in seagrasses and algae. Today, as green sea turtle populations have declined, these food resources are unlikely to be depleted (Bjornal et al. 2000).

Adult green sea turtles make long breeding migrations that can be several hundred kilometres long. They move between food areas and nesting beaches, although the migration activity is long and not continuous. Green sea turtles have their residence in a particular environment tied to a particular feature. Research has shown that juvenile turtles, for example, move in a planned pattern between daytime foraging areas and nocturnal resting areas. Longer movements could occur in juvenile turtles during seasonal migrations. Green sea turtle sexual maturity is estimated to be between 20 and 40 years of age, depending on growth rates in the wild. Higher growth rates have been

shown in estuaries, probably due to the availability and abundance of food. In general, green sea turtles grow more slowly with age and stop growing altogether as adults. Growth rates vary with geographic location, and it is difficult to determine their age at maturity, with some authors believing that accurate age determination is impossible (Witherington et al. 2006).

1.2.5. Threats

The threats to sea turtles and the potential risks of extinction are very similar worldwide. In addition to threats from various predators in the animal kingdom, humans can also be considered a major predators. Human activities such as oil extraction, fishing, use of plastics, coastal lighting, etc. The impact of the developing industrial society along with the construction of cities and tourist centres is certainly one of the reasons for the listing of sea turtles as an endangered species in the year. This occurred in the USA in 1978 and was an important factor in the initial recovery of the population (Polovina et al. 2003).

More recently, artificial lighting near nesting beaches has been an acute concern. Female green sea turtles are discouraged from going out onto the beaches to nest and the light reduces the ability of hatchlings to find the ocean. Instead of following the light caused by ocean glare, they follow the wrong direction for illumination. Research has shown that light smog modifies spatial nesting patterns and causes mass mortality of hatched young (Salmon et al. 2000). A different author describes another serious problem caused by beach lighting. Misdirection on the way to the sea can cause dehydration, exhaustion or death in newly hatched turtles due to predators (Berry et al. 2013). On Florida beaches, for example, research has shown that approximately 20 % of nests have been recorded as having poor nestling routing. Instead of heading out to sea for lighting. Although clear and precise mortality resulting from misrouting has not been demonstrated, it is estimated that up to 50 % of hatchlings die in this manner. This represents 10% of the total number of hatchlings (Hirth 1997).

Another serious problem is fibropapillomatosis, a cancerous growth on the skin and internal organs. This disease was reported as early as the 1930s, but there have been no known cases in recent decades. Now the disease has returned and fibropapilloma tumours are relatively frequent in the green sea turtle and are also occurring periodically

in the loggerhead species. Tumours growing on the skin and eyes of turtles can be as large as 30 cm (Humber et al. 2011). Based on research, the Indian River Lagoon and Florida Bay estuaries have been identified as hotspots for the disease. Although the disease is not malignant, these tumours have had an impact on the weakening and subsequent death of the turtles. Survival rates of infected turtles have never been precisely defined, but turtles with fibropapillomas were more likely to be emaciated, weakened, dead, or entangled in trash and plastic (Witherington et al. 2006).

Efforts to protect sea turtles are now seen around the world, and the green sea turtle population is listed as endangered under the criteria of many organizations. Governmental and legislative regulations have banned the direct harvest of green sea turtles, many places have banned the use of nets on the coast or are regulating local beach lighting ordinances, unfortunately, compliance with these local laws is not always 100%. Long-standing international agreements such as the CITES and the Convention on the Conservation of Migratory Species of Wild Animals (CMS) could be of great help. These establish worldwide conditions for the commercial and indirect commercial harvest of sea turtles (Rusli 2019).

1.3. Light perception

Earlier authors Hendrickson (1958) and Bustard & Witherington et al. (1990) described the first visual perceptions of hatchlings. The initial phase of green sea turtle life takes place on land and is not very long. When the hatchlings emerge from the nest, they reach the seawater within a few minutes, if nothing disturbs their efforts. The vast majority of hatchlings have their first visual experience at night. So, their first light conditions can be influenced by the weather of the moment, from a bright full moon to an overcast sky (Hendrickson 1958; Witherington et al. 1990).

Wyneken et al. (2013) also investigated the light perception of green sea turtles. They described when light contacts occur on land. This happens in adult females that come onto beaches primarily to lay eggs, mostly at night. Visual orientation on the nesting beaches is their main visual task. Further contact with light takes place just above the surface during respiration. Because sea turtles breathe air, they spend some

part of their lives at the surface where they can observe the visual scene above the water.

From the above, it is clear that the visual system of sea turtles is exposed to different light environments. Lohmann et al. (1997) concluded that vision in murkier coastal habitats or clear ocean waters probably is crucial for sea turtles. They occur in both environments but sometimes prefer clear water, depending on different activities. Feeding, avoiding predators and finding mates are important to them. Sea turtles move in a wide range of light intensities. For example, sea-finding for sea turtles on nesting beaches occurs mostly at night and feeding occurs mostly during the day. All of this affects the design of the eye, along with the fact that sea turtles evolved from terrestrial ancestors (Hirth 1997).

Sea turtles belong to a group of vertebrates in which vision has evolved to the highest level of complexity. Sea turtles have a range of visual system functions to adapt to a terrestrial but mainly aquatic way of life. This topic has been the subject of much research, yet knowledge of the visual abilities of sea turtles is limited. Bartol and Musick (2002) focused on studies on the visual abilities of the green sea turtle.

Johnsen (2006) was interested in describing the main sources of light on Earth, given the diverse exposure of sea turtles to light on land and in the sea. Sea turtles can perceive light either as direct sunlight during the day or as a reflection from the moon during the night. The authors report that the intensity of daylight at the sea surface can vary by up to 10 orders of magnitude between day and night. The presence or absence of the moon, cloud cover and the intensity of the radiation varying during the day also play a big role. The most significant changes are seen around dusk and dawn.

Clarke and Denton (1962) attempted to measure the spread of light through water, its absorption and scattering. Light intensity, colour and contrast change significantly as it passes through the ocean. All of these affect the visual contact of sea turtles with light. For example, at a depth of 500-700 m during the day, the light intensity reaches starlight levels; at a depth of 1000 m, almost no daylight is visible. Most turtles are found in the upper depths of the ocean, most often in the water column 200 m below the surface. In this area, there is bright spatial light. Daylight is visible in all directions around the turtle because particles suspended in the water scatter daylight in all directions. An animal floating near the surface will thus see light coming from

below, from the sides and, of course, from above. With increasing depth, however, the spatial intensity of light visible from below and the sides decreases, and the available daylight comes increasingly from above.

Jagger and Muntz (1993) investigated the spatial light intensity in relation to the visibility of objects in the sea and concluded that spatial light has an adverse effect on the contrast and visibility of objects in the sea. The scattering of daylight falling downward creates a veiled haze of space light in which an object may be poorly visible. Such scattering reduces the contrast of objects and shortens the distance at which an object can be seen. The farther away the object is, the greater the volume of water between it and the observer, and the greater the number of suspended particles that scatter light into the observer's field of view. As the object gets farther away, this scattered light eventually becomes brighter than the light from the object reaching the eye, and eventually completely obscures it. For a dark object in clear ocean water, as early as 40 meters away, the visual contrast of the object drops to zero and the turtle no longer sees the object.

The visibility of objects is greatly influenced by both the properties of the water and the bioluminescent signals of aquatic organisms, which together create a luminous environment. This light environment is readily visible to turtles at upper depths, but the environment changes greatly with depth. In the lighter upper depths, visual scenes are expanded, with light entering the eye from objects that are in the visual scene in all directions. The scattering produces a uniform blue spatial light, and in coastal waters, the seafloor may be visible. However, at depths, the spatial light diminishes, and bioluminescent point sources begin to appear, especially from below where the spatial light is weakest (Warrant & Locket 2004).

1.3.1. Visual apparatus

Wyneken (2001) was involved in research on the vertebrate eye. The main function of the vertebrate eye is to provide support and structure for the transmission and focusing of incoming light. Light strikes the retina which processes it. The nerve tissue lining the back of the eye transmits light information to higher visual centres in the brain. The eyeball is filled with fluid, with the aqueous and vitreous humours forming a clear medium that maintains the shape of the eyeball and keeps the retina in

focus. In sea turtles, the eyeball moves independently of head movement, using six extraocular muscles. Sea turtles have a third eyelid, the nicotine membrane, which protects and moistens the eye (Hudson & Lutz 1986).

Light enters the sea turtle's eye through the cornea, whose curved and refractive surface acts as an interface between the air and the watery environment inside the eye. Underwater, the cornea loses its refractive power and functions only as a protective barrier, the refractive power being provided by the globular lens. The corneas and lenses in animals are adapted to the environment in which they live. For example, freshwater turtles have a curved cornea and a relatively flat lens, this allows for more frequent vision on land. Sea turtles, on the other hand, have nearly spherical lenses and corneas with little curvature. They need this for their predominantly aquatic lifestyle (Northmore & Granda 1991).

Northmore and Granda (1991) examined the optical abilities of sea turtles in detail and concluded that sea turtles are myopic in air and hyperopic in seawater. They also suggest that they are capable of accommodation, a view shared by the other authors. Brudenall et al. (2008) describe well-developed iris-expanding muscles that help the iris to change size. This may assist the eye's accommodation by compressing the front of the lens. In addition to its accommodative function, the iris may help regulate the amount of light entering the eye. Sea turtles have a retina divided into seven layers (Bartol & Musick 2002; Brudenall et al. 2008). Due to developmental constraints in vertebrates, the retina is inverted, with the light-absorbing photoreceptors facing away from the incoming light. The pigment epithelium forms the outer layer adjacent to the choroid. The photoreceptor layer in sea turtles contains both rods for twilight vision and cones for bright light vision.

Light sensitivity was investigated by Howland (2004) and his team, and they focused on how the turtle can respond to bright and dim light. The turtles' optical apparatus is capable of collecting light, perceiving acuity and relaying information to the brain. However, the results of the studies showed that the sea turtle is not ideally adapted to dim light conditions because its eyes are relatively small due to its large body size.

Other authors agree in describing the eye as very small compared to the sea turtle's body. The lens and pupil are also relatively small relative to the size of the eye. Because of these circumstances, light flows into the eye through a relatively small slit and there is a reduction in retinal illumination. Even though this research was conducted on different species of sea turtles, the results proved to be the same for the green sea turtle. The research confirmed that the anatomy of the eye is adapted to the turtle's daytime life (Northmore & Granda 1991; Brudenall et al. 2008).

The consensus of the authors was through studies of light sensitivity in the sea turtle eye. It demonstrated a duplex retina, meaning a fairly balanced representation of rods and cones. Most sea turtles do not have specially adapted eye anatomy to see during night or twilight; they see better during the day. Research has shown that turtles use dim light for orientation when searching the sea (Wyneken et al. 2013).

1.3.2. Object and light perception

Bartol and Musick (2002) focused on examining the visual acuity of sea turtles in the water and on land. The density and distribution of photoreceptors and ganglion cells is a major determinant of visual acuity, with the overall optics of the eye playing a role. The extremes of visual acuity have been investigated. In their experiments, the team got sea turtles to distinguish between grey and striped panels. Acuity was measured by increasing the number of stripes on the panel until the turtle distinguished the striped panel from the grey panel. Green sea turtles exhibited an acuity threshold of 0.078, that is, approximately 5 cycles of black and white bars per degree of visual angle. To compare with the human eye, humans in a similar experiment showed 60 cycles per degree, that is, a much higher visual threshold. These values indicate acuity to visual stimuli in water (Bartol & Musick 2002).

In contrast, acuity experiments measured on land have shown less acuity and therefore poorer spatial perception. Researcher Witherington (1992) concluded that juvenile sea turtles perceive visual stimuli over a relatively large spatial range, with the visual field representing approximately 180 degrees of their perception. Bartol and Musick (2002) attempted to compare the vision of sea turtles on land naturally and then with seawater-filled goggles on, thus restoring visual perception in water. The result showed that turtles without goggles did not respond to stimuli nearly as well as turtles with goggles. This means that the visual apparatus of sea turtles is not sufficiently

adapted to sharp vision. Thus, on land, sea turtles have reduced spatial recognition ability, but this does not mean that they do not respond at all (Brudenall et al. 2008).

In the past, several research teams, such as Limpus (1971), van Rhijn and van Gorkom (1983) and Salmon et al. (1992), have investigated the responses of hatchling sea turtles to sea-finding. They showed that turtles respond clearly to a variety of shapes, objects and silhouettes that do not require high visual acuity. The results of their study proved that hatchlings perceive both horizontal height differences and vertical contours of objects. Later research by Levenson et al. (2004), revealed and measured sensitivity to light stimuli in green sea turtles. However, this area would require further investigation. The results showed that hatchlings and adults of the green sea turtle have a response to ultraviolet light at wavelengths below 400 nm, which is not visible to humans. The lens of sea turtles transmits greenish light in the ultraviolet range, which is not common in other animals. This demonstrates that sea turtles respond to ultraviolet light, but it does not mean that they can distinguish the colours of UV light from other wavelengths (Mäthger et al. 2007).

The response of hatchling sea turtles to different types of light has been investigated. The authors of the studies focused on what light sea turtles prefer according to different wavelengths. Hatchlings have been shown to go for shorter wavelength light, like which is blue, violet and ultraviolet light. This behaviour has also been observed in adult green sea turtles (Berry et al. 2013). Other authors studying sea turtles have come to the same conclusion. Moreover, Salmon and Witherington (1995) demonstrated in their studies that green sea turtle orientation is better at night in the moonlight, regardless of where the moon is in the sky.

Most animals on Earth perceive natural light as highly polarized and have the ability to see it. Green sea turtles are also able to sense this light produced by sunlight or moonlight. How it serves them to orient or navigate in nature is still being studied (Horváth & Varjú 2004). A logical explanation is offered that polarization vision helps green sea turtles find their way to the sea on the beach. However, earlier experiments showed that green sea turtles do not lose their orientation when provided with depolarizing goggles. This means that even without polarized light they can find the sea without any problems. Later, studies of sea orientation in hatchling green sea turtles were carried out. They showed that the young did not maintain swimming direction

even with a bright polarized light pattern and did not use it as a guide. (Irwin and Lohmann 2005). The reason for this may be that newly hatched turtles cannot distinguish polarized light. Other authors, on the contrary, are of the opinion that these light signals are not used during the period called swimming frenzy because of the predominance of other sensory perceptions. Also, the intensity and composition of the light signal may influence the outcome (Kamrowski et al 2015).

These facts suggest that juvenile green sea turtles can use their entire sensory system to find the open ocean. It is remarkable how the newly hatched creatures can orient themselves, but it is not without some visual cues. As discussed in the previous chapter, visual acuity is low for seeing on land, yet the hatchlings are able to find the ocean. General research results show that spatially prominent cues, such as a wide dune on the beach or the light shade of the ocean horizon, help them to do so. On a clear night, when there is plenty of moonlight, the ability to find the sea is higher than under overcast skies. A brightly lit horizon is a good guide signal (Mäthger et al. 2007; Brudenall et al. 2008).

1.3.3. The influence of artificial lighting

Although sea turtles have inhabited our planet for more than 110 million years, the last century has seen significant threats to the species. One of the main threats is ever-increasing light pollution. Night-time lighting of the coastline has become a new threat, a new type of pollution that has a significant impact on the environment of the organisms living there. The area of Florida with its nesting beaches has been the subject of research. Florida is one of the most abundant areas for the green sea turtle. Studies have focused on the possible influence of artificial lighting on sea turtle behaviour. The greatest threats from artificial lighting can be divided into several areas (Hu et al. 2018).

One of the areas is green sea turtle nesting and incubation. A possible link between artificial lighting and nest density was assessed. The results showed that artificial lighting affects sea turtle behaviour in several ways. It was found that already when searching for a nesting beach, female green sea turtles prefer darker environments to illuminated beaches. Of course, the intensity of the lighting has an effect, the brighter the environment the more the likelihood of nesting decreases (Salmon et. al 2000). It has also been found that false crawling can occur, where a female adult turtle will come

up onto the beach to nest but quickly return to the sea without digging up the nest and laying eggs. Searching for less lit or unlit beaches by nesting females leads to higher concentrations of nests in dark environments. This may result in lower numbers of hatchlings and may also result in nest destruction by other females. It also increases the likelihood of predation and deprivation of young (Pilcher et al. 2000). Another risk is that artificial lighting may be perceived by sea turtles as daylight, and thus may inhibit nocturnal behaviours associated with nesting. Also, nesting turtles are more likely to be disturbed by humans on lighted beaches than in the dark. When disturbance occurs, egg laying is interrupted, or the entire nesting process is aborted (Hu et al. 2018).

Another area focused on orientation. Previous studies had already revealed disorientation in experimental turtles that moved mistakenly to a source of artificial lighting or crawled in circles. This unnatural light causes an artificial light trap. Unlike moonlight and sunlight, it tends to be directed to one location and does not illuminate the surroundings much. Turtles hatched on a dark night are unable to find other light signals and move in the wrong direction, falling into a light trap (Salmon and Witherington 1995).

More recently, Booth and Evans (2011) described how artificial lighting has a significant effect on the orientation and subsequent movement of hatchling sea turtles. Once hatchlings emerge from the nest, they begin to perceive landmarks that help them to navigate their way to the sea. The perception of space is influenced not only by photopigments and oil droplets in the retina but also by the colour and shape of the beach. On a normal night in uninhabited areas, the sea horizon is significantly lighter in colour than the land, the route of the young is focused on the ligand ht, they are likely to reach the sea surface. The light of the moon or stars reflecting off the ocean surface is a sufficient guide. In the case of artificial light, there may be a problem. If young green sea turtles perceive it as a brighter point than the sea surface, their path may be inland. Poor orientation means a significantly higher mortality rate of juveniles due to predation, dehydration or exhaustion (Lorne & Salmon 2007).

The next area where sea turtles are threatened by artificial lighting is the circadian rhythm of these animals. Circadian rhythms are very important for all organisms on the planet as they influence physiological processes and biological activities. To illustrate, it affects sleep, body temperature, metabolism, hormone

production, brain activity, etc. The distinction between day and night is very important for animals. If there is an imbalance between the internal biological clock and the external environment, the circadian balance is disturbed. For example, when a sea turtle, due to artificial lighting, thinks it is a day at night. Natural night light promotes the production of melatonin, which acts as an antioxidant and provides immunity. In the case of its deficiency, health problems could arise, leading to a decline in the sea turtle population (Jones et al. 2015).

The findings of research investigations have become the basis for legislative documents leading to the protection of sea turtles. These include regional ordinances and regulations commanding the limitation or turning off lights. The authors of the studies agree on several effective measures that would eliminate the impact of light on nesting beaches and reduce hatchling disorientation. Examples include various shielding, partially turning off lights, or using different wavelengths. Also planting shade trees and shrubs or creating artificial dunes where the light would not be as visible.

For example, Witherington et al. (1990) described how the intensity of artificial lighting can be influenced by the style of development, the vegetation growing or the season. Enclosing private properties with walls or lush vegetation can act as a light barrier. Artificial beach lighting may be different at various times and seasons. Tourist season, occupancy of buildings, or simply leaving lights on in garages and front of houses can have an impact. Also, a nearby highway or another road may influence animal behaviour by the lights of passing cars. Research showed that female sea turtles will nest mostly after midnight when most people have their lights off. In contrast, according to the authors of the study, most hatchlings emerge between dusk and midnight. Their ability to find the sea varied by location, with disorientation greater in areas with little or no vegetation cover. Misorientation was also caused by differences in horizon height.

The impact of each particular solution is the subject of long-term studies and research (Tuxbury & Salmon 2005).

1.4. Situation in the study site

1.4.1. History of Tortuguero

The environment is a subject of growing concern about the protection of fauna and flora. Most countries in the tropics have adopted a range of legislation to protect their fauna. One effective step appears to be the establishment of national parks. A very valuable system of national parks has been established in the Costa Rican region, especially in the last decade. However, some national parks have a long history. On the northeaster Caribbean coast of Costa Rica, the Tortuguero National Park was established as early as 1975 (Place 1988).

Tortuguero National Park has 20,000 hectares of forested area and a 35 km long beach. During the nesting season, from approximately March to October, four species of sea turtles nest here. These are greens, leatherbacks, hawksbills and loggerheads turtles. For the purposes of my thesis, I will focus on the green sea turtle, which is the most abundant species. They are also a highly endangered species. The Tortuguero region is generally considered the most important nesting beach for this species in the Western Hemisphere. Between 17,400 and 37,290 females regularly arrive here each year to breed (Gutiérrez-Lince et al. 2021).

The climate here is ideal for abundant vegetation and animal life. This is the wettest part of Costa Rica, which is rich in rainfall and knows almost no dry periods. This climate, favourable for animals, was not ideal for building infrastructure so that in 1975 there was only one population living here, and that was in Tortuguero village. The inner part of Costa Rica was an uninhabited area with swamps, marshes and forests (Place 1988).

The history of Tortuguero is linked to the occurrence of the Caribbean green sea turtle, even the name comes from the Spanish word for turtle. The turtle was an important source of food for the people of the village, providing them with plenty of meat and eggs. When Tortuguero was first settled, before 1500, the people needed natural resources to survive. Sea turtle meat and eggs were their main food. 200 years later, Tortuguero was famous among traders and sailors for its high number of nesting turtles. An economically viable trade in everything the turtle had to offer began to develop. Meat, eggs, shells, and oil were traded (Tröeng & Ranking 2005).

In the 20th century, the sea turtle trade reached widespread importance, with turtles regularly harvested from the area by huge ships. The hunt was mainly for green sea turtles, the fatty mass extracted from the area under their carapace was the source of the food used to cook turtle soup. Caught turtles were sold at a port 80 km away. Exports were concentrated in Europe and North America where the soup was in demand. The meat and eggs remained on the domestic market and became an important trade item. Unfortunately, the local sea turtle population was almost wiped out. Among the earliest attempts to save them was the work of conservation biologist Dr Archie Carr. He was behind the research that monitored the nesting behaviour of the green sea turtle on the beach at Tortuguero. During the research, he employed local villagers to help him tag the turtles. Thus, for the first time, the green sea turtle generated a financial gain of a non-consumptive nature. The biologist's work reached its peak in 1959 with the founding of the Caribbean Conservation Corporation, later called the Sea Turtle Conservancy. This organization was very influential in the establishment of Tortuguero National Park (Gutiérrez-Lince et al. 2021).

Over time, the research activities of the nesting population became known, and the general public became interested in sea turtle conservation. There was growing concern about the depredation of sea turtle populations for trade. Efforts to protect sea turtles became evident. Several environmental groups and organizations became involved. In the 1960s, many countries adopted legislation to prevent the trade in sea turtles. Several laws were introduced to protect these magnificent creatures and to prevent the international and domestic trade in turtle products. Today, turtles in Tortuguero are only subject to research, environmental and tourism activities that can also support the local economy (Meletis 2007).

The origins of Tortuguero National Park in 1970, with all its environmental regulations, meant that local people had limited access to natural resources. Previously accessible management became complicated. Many people left to find work elsewhere. Others struggled to make a living growing crops and fishing. The national park with its conservation activities had a positive impact on the sea turtle population but a negative impact on the standard of living of the local people. Livelihoods and fundraising were quite difficult in Tortuguero. Lack of infrastructure limited access to the village and Tortuguero remained disconnected from Costa Rica's developing economy. It took until

the opening of a canal between Laguna del Tortuguero with an inland waterway leading from Limon. This canal represented the village's connection to Costa Rica and through it, Tortuguero began to develop economically (Place 1988).

The creation of the canal has led to economic growth, which has meant more visitors and a higher standard of living for the local population. Many of them became guides for incoming tourists who wanted to see sea turtles laying eggs on the beach. Tourism focusing on sea turtles as a protected species also slowly changed the mentality of the local people who began to appreciate the natural resources in this beautiful area The development of tourism has gradually brought a negative impact on sea turtles. During the nesting season, there were so many tourists on the beaches that green sea turtles lost their peace and privacy. The behaviour of incoming visitors was not controlled in any way, nor were their numbers limited. Tourists disturbed the nesting turtles with noise and light from their flashlights and cameras. The locals started to organize the movement of tourists along the beach and helped them to find the turtles for a small fee. Thus, the Sea Turtle Guides Association was formed to organize guiding services to mitigate the negative impact on the turtles (Gutiérrez-Lince et al. 2021).

Over time, however, the number of tourists visiting Tortuguero has increased and thus the pressure on sea turtles has grown. Research studies have shown changes in their behavior. For example, false nesting, where a turtle leaves tracks on the beach indicating nest construction but does not nest, has been recorded in areas with more tourism. Again, other measures to protect sea turtles have been put in place. In 2004, the turtle tourism system was changed, and the Ministry of the Environment and local communities tried to reduce disturbance to nesting turtles. The new system consisted of observers patrolling the beaches themselves and taking tourists to the turtles only at the appropriate nesting stage. This reduced the time outsiders were on the beaches and resulted in higher numbers of nesting turtles. At the same time, a new job opportunity for Tortuguero residents was created in the form of observers. In 2019, there were 14 of these observers and the number has gradually increased (Tröeng & Ranking 2005).

Despite all efforts, disturbance to nesting turtles has not been sufficiently reduced. Tourists, in an attempt to take pictures with the hatchlings, illegally dig nests, through local people or even guides. Money can buy similar services in these areas, and this is probably the biggest problem at the moment. The changes made to protect sea

turtles have never been fully accepted in the Tortuguero community, even though it often financially helps the residents. It can be considered a success that nesting turtles have a safer environment on Tortuguero beaches than they did sixty years ago (Meletis 2007).

1.4.2. Effects of artificial lighting on sea turtles in Tortuguero

As described in the previous chapter, tourism has gradually developed. As a result of this situation, the intensity of light smog has also increased, and this has happened all over the planet. The development of society, industry and tourism has meant that the human population has changed the level of night lighting. Bird et al. (2004) estimate that light pollution affects 20 % of the land surface. Other authors Gaston et al. (2012) and Hölker et al. (2010) believe that light pollution is increasing globally by approximately 6 % per year.

Artificial light that changes the natural cycles of light and dark in ecosystems is referred to as ecological light. It can significantly affect animal behaviour by altering spatial and temporal orientation signals (Longcore & Rich 2004). All animals living freely on our planet are guided by the internal biological clocks that were given to them in ancient times. Light smog can significantly disrupt this internal balance. Also, light points are important clues for them; if the light is artificial, it can pose a significant threat to the animals. In general, a change in the natural light regime means a negative effect on the communication, migration and reproduction of animals. Foraging activities and habitat use are also affected, and predation and mortality rates increase (Gaston et al. 2012). It is evident that this topic has been addressed by several authors, however, for the purposes of my paper, I will focus on research conducted on sea turtles in the Costa Rica-Tortuguero region.

Since 2004, research activities have also been carried out on the nesting beach near the village of Tortuguero. Studies have focused on artificial lighting and investigated its effect on nesting female green sea turtles. The infrastructure built, the development of industry and ecotourism have increased annual visitor numbers and also meant the development of the Tortuguero town. Not only has development expanded in the village, but also to the north of the town where tourist cottages and lodges have been

built near the beach. All of these residences had artificial lighting and had an impact on the nesting behaviour of the green sea turtle (Constant 2015).

1.4.3. Effect of artificial lighting in Tortuguero on sea turtle nesting

The effect of artificial lighting on sea turtle life has been studied and described by Bir et al. (2004), Longcore and Rich, (2004) and Witherington and Martin (2003). In general agreement, they documented the negative effects of artificial lighting on sea turtle populations. The results showed how artificial lighting alters sea turtle nesting behaviour.

According to research studies in the Tortuguero region of Costa Rica, the situation is similar. The local sea turtle population tends to nest at certain recurring periods. It is a seasonal thing and females nest repeatedly on beaches during one season. Sea turtles nest on sandy beaches mostly at night and lay their eggs above the high tide line. The authors of Witherington and Martin (2003) describe the nesting process as a systematic and deliberate activity that can be disrupted by artificial lighting. Nesting begins with the female emerging from the sea and locating a nesting site. Already at this stage, natural behaviour can be disrupted, with artificial light preventing females from finding suitable nesting sites. Either they do not come out of the sea at all, or false nesting occurs. If the female is not disturbed by lighting, nest site preparation follows by body pitting. The next part of the process is excavating the egg chamber and laying the eggs. Finally, the female covers and camouflages the eggs with sand. She tries to orient the nest towards the water and when she is satisfied, she returns to the sea. (Hendrickson 1995).

The situation described may not always be exactly within this timeframe. Female behaviour can vary according to many circumstances. It depends on where she emerges from the sea, where she builds her nest, and whether she is disturbed by light, predators, or humans. Clear or cloudy skies also play a role. These external circumstances, including light smog, can affect nesting behaviour. These facts were previously confirmed by the research team of Witherington and Martin (2003) who documented how artificial lighting interferes with sea turtles' choice of nesting beach. The result confirmed less interest in nesting on brightly lit beaches. Females are

discouraged from coming out of the water to nest or leave the beach in search of a darker environment. The researchers mentioned above also conducted an experiment. This involved manipulating the brightness directly on the beach and it was shown that in the absence of other distractions, this artificial brightness significantly reduced nesting activity. It depended on what intensity of brightness was used (Witherington & Martin 2003).

Due to disturbing elements, the selection of nesting sites for females is becoming more and more challenging, they try to select favourable sites for safe nesting and production of young. Artificial lighting can lead females to search for unlit areas where they climb to less suitable nesting sites. This use of otherwise suboptimal habitats means that sea turtles lose their normal nesting habitat due to light smog (Constant 2015).

1.4.4. Effect of artificial lighting on sea turtle orientation

Like other animals, sea turtles use visual light signals to navigate on land and in the sea. This ability is not only present in adults but is natural and necessary for hatchlings just after hatching (Limpus & Kamrowski 2013).

Describing the behaviour of hatchlings in the wild, far from civilization, represents natural behaviour. Immediately after emerging from the nest, a rapid crawl towards the ocean is followed by an orientation to a brighter horizon. Sea turtles are attracted to light with shorter wavelengths and in natural conditions, this light is most prominent towards the sea, this allows them to find the surface. If they get to the sea safely, they start swimming furiously. They navigate in the sea using waves, magnetic signals and brightness (Tuxbury & Salmon 2005).

In the case of artificial lighting, which is in visual proximity to the nest, a completely different situation occurs. The orientation of the hatchlings is disrupted by this light smog. Since it is also a short wavelength, it is natural that they confuse artificial signals with natural ones. The ability to sense the sea and head in the right direction is affected. Either the hatchling orientates incorrectly to the artificial light and goes in that direction, or it loses its orientation completely and moves, for example, in circles (Lorne & Salmon 2007; Berry et al. 2013). This disorientation has been found in both high and lower light conditions, which they may perceive as natural signals. These

can be distant and relatively unnoticeable light sources, perceived by turtles as light reflecting off the sky or sea surface, or direct point sources clearly visible from the beach (Harewood & Horrocks 2008).

As already described this disorientation is very dangerous for hatchling sea turtles, and research in Tortuguero has confirmed this fact. Mortality of turtles is increasing, the reason being predation, dehydration or exhaustion during a journey that does not go as fast to the sea surface. Artificial light does not provide the young with good direction, and they may die or wander for longer periods while searching for the sea, increasing the likelihood of mortality. Also, moving in circles where orientation is strongly disturbed by artificial light leads to rapid energy consumption and again risks mortality (Witherington & Martin 2003). Unfortunately, juveniles with poor or no orientation are more at risk even after reaching the sea. The results of Harewood and Horrocks (2008) study showed, that disturbed orientation by exposure to artificial lighting affected the behaviour of hatchlings after reaching the sea. Due to the large loss of energy during wandering, their life was at significant risk. Because they no longer had sufficient energy reserves, they were tired and much slower, thus being more at risk from predators, which are more abundant in coastal areas than in the open sea. Wandering on the beach consumed some of the energy that was missing during the demanding swim in the sea.

Aims of the Thesis 2.

The main aim of the thesis was to investigate how artificial lighting affects the

orientation of sea turtle hatchlings.

The specific aim was to research a specific area of nesting beach, during which I

observed green sea turtle hatchlings released from arenas exposed to different lighting

intensities. I recorded their movements and investigated their level of disorientation

while finding their way to the sea under different levels of public lighting.

Another objective was to determine how disorientation rates changed after

replacing public lighting with sea turtle-friendly lights. For logistical reasons, it was not

possible to analyse the second aim. STC is looking to obtain results from that study

soon. Therefore, this study serves as a baseline and recommendation for further research

conducted by STC on this topic in the future.

Hypothesis: Disorientation of hatchlings increases with increasing artificial light.

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3. Methods

3.1. Study site

The study site was Tortuguero beach, on the northern Caribbean coast of Costa Rica, in the province of Limón (Figure 14). The black sand beach is approximately 29 km long and it is located between the Tortuguero and Laguna de Jalova River mouths (Neeman et al. 2015). According to the STC, the beach is divided into the Boca section, located north of the STC station, starting at marker 4.2 and ending at marker -0.6, where the mouth of the Tortuguero River is located. The other part is called Park, situated between marks 4,2 and 8,0 to the south. Tortuguero town lies mostly between markers 5.4 and 4.2. The National Park is to the south of the town and begins at marker 5.4 and ends at marker 8.0.

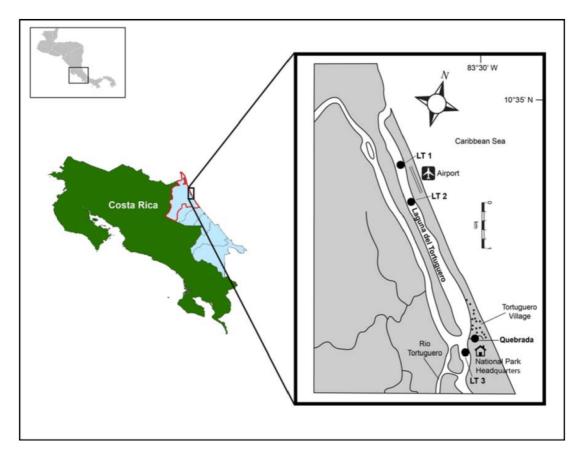


Figure 14. Study site in Tortuguero, Costa Rica (Petra Kranzfelder, 2012).

3.2. Experiment design

The hatchlings of green sea turtles were collected from wild and marked nests every morning from 6 a.m. Of the wild nests, the ones from which the hatchlings had already emerged, which was evident from the tracks leading from the nest, were of interest. These nests were then excavated and the remaining hatchlings in the nest were collected. Or those in which the young had already hatched but had not yet begun to crawl to the surface, these nests can be identified by a sinkhole in the sand called a "depression". The hatchlings were also obtained by research assistants from marked nests during the morning survey, on the day they would naturally emerge. A maximum of 20 hatchlings could be taken from each nest so that the nest is not disturbed, and the rest of the clutch was left to crawl to the sea naturally. The captured turtles were transferred in boxes to the STC laboratory within a few minutes. They were stored in a dark part of the room at outdoor temperatures until it was used the same evening for the experiment.

The whole research took place in the Park side, between markers 4.2 and 5.4, as there is a town with lighting on this part of the beach that makes the turtles disoriented. There is no evidence of disorientation on the Boca side. All observations and experiments were carried out between September and October 2021 during the rainy season. The study site was a 1.2 km long section of beach bordered on one side by vegetation and the other by the sea. Disorientation experiments were conducted every 100 meters in front of the town. For a distance of 1.2 km there were 13 arenas repeated twice, so 26 arenas in total.

The starting point was in front of the STC station (marker 4.2), where there is no lighting, continuing towards the town as the lighting rises, and ending in the national park where lighting drops to none (marker 5.4). Each experiment contained 20 hatchlings, a Sky Quality Meter luxmeter, a Garmin eTrex 10 GPS, a compass, flags, a meter, a protractor, and template sheets.

Hatchling-orientation data were collected using circular arena trials. Each observation started by drawing a 3 m radius circle ("beach arena") in the sand, which was then by using a protractor divided by 15° into 24 sections (Figure 15). Sectors (1–24) proceeded in counter-clockwise order around the arena, with sector 1 being most seaward. In the middle of the arena, the light intensity was measured using a Sky

Quality Meter, in 4 directions: north (Boca), east (sea), south (Park), and west (vegetation). Each measurement was noted in a template table and repeated three times to calculate the average of these three measurements. The angle from north to sea was also measured with a compass and the location was taken using a Garmin GPS in the middle of the arena.

Before placing the hatchlings, the surface inside the arena was smoothed and cleaned to make it easier to follow the tracks. All 20 green sea turtle hatchlings were released from the centre of the arena. The turtles were set free in numbers of 5 by removing them from the box with gloved hands and putting them in the sand. After approximately 20 seconds, a red light was briefly turned on to determine whether they had left the arena. Tracks in the sand were followed and the crossing of the arena was marked with a flag. Hatchlings moving towards the town were captured and released again. Turtles that crawled in the correct direction to the sea were let go. After the five individuals left the arena, the sand was smoothed again to erase the previous tracks so that the tracks of the other five specimens could be followed. After all, 20 hatchlings were released, the number of flags in each sector was counted and recorded in a sample table (Table 1).



Figure 15. Circular arena divided into 24 sectors pictured in daylight (Tereza Znachorová, 2021).

Arena					Arena	1							
Date Marker			30.09.2021										
warker			Databa	ness Readi	4.2		Т	COMPACE					
	COMPASS												
		in mag/arcsec ²				in μcd/n	70°						
		1	2	3	1	2	3						
MAR		19.70	19.80	19.68	1423.72	1298.45	1450.19						
BOCA		19.82	19.88	19.84	1274.75	1206.21	1251.48						
VEGETATION		19.54	19.68	19.66	1649.77	1450.19	1477.15						
PARK		19.59	19.56	19.54	1575.52	1619.66	1649.77						
MOON LIGHT		NO											
GPS		N 10°32.899'											
			W 083°30.	284'									
Section	Tracks		Comments										
1	4												
2	4												
3	3												
5	1												
21	1												
22	3												
23	2												
24	2												

Table 1. Example table showing the way of recording data.

3.3. Study analysis

All statistical analysis were done using R studio - Version 1.3.1056. Package "circular" was used for a circular data computation. A Rayleigh test was used as a test for significant unimodal orientation, e.g. Is each turtle in the treatment going the same direction?

4. Results

All statistical analysis were done using R studio - Version 1.3.1056 (Table 2). Package "circular" was used for a circular data computation. A Rayleigh test was used as a test for significant unimodal orientation, e.g. Is each turtle in the treatment going the same direction?

Arena	Test statistic	P-value	Arena	Test statistic	P-value
1	0.8641	<0.05	14	0.8047	<0.05
2	0.8664	<0.05	15	0.869	<0.05
3	0.2386	0.3244	16	0.8859	<0.05
4	0.4841	<0.05	17	0.2912	0.1847
5	0.9353	<0.05	18	0.5953	<0.05
6	0.9098	<0.05	19	0.7985	<0.05
7	0.6594	<0.05	20	0.3834	0.0509
8	0.7135	<0.05	21	0.7365	<0.05
9	0.9306	<0.05	22	0.9161	<0.05
10	0.3614	0.0718	23	0.9915	<0.05
11	0.6539	<0.05	24	0.9373	<0.05
12	0.8127	<0.05	25	0.8024	<0.05
13	0.4034	<0.05	26	0.9071	<0.05

Table 2. Results after using R studio - Version 1.3.1056

In some arenas, there was no obvious influence of artificial lighting, and all the hatchlings were facing the right direction into the sea. In some arenas, however, the degree of disorientation was very noticeable. Disorientation was less or almost absent for arenas that were located on a part of the study area with no lighting, or artificial lighting was hidden by vegetation. As can be seen in arena 1 (Figure 16) and 2 (Figure 17), where the same dispersion is 120° and all turtles went in the right direction. The tracks in each arena are colour-coded blue (if the hatchlings headed between 300° and 60°) orange (if the cubs headed between 120° and 240°) and red (if the cubs headed above 120° and 240°). In each arena it is marked where north is located and the direction from which the greatest illumination comes is shown by a yellow circle. Also, the brightness measured in all world directions is shown in mag/arcsec² and μ cd/m² in each arena.

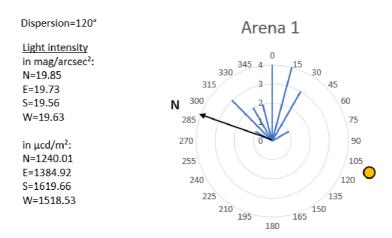


Figure 16. Arena located on an unlit part of the beach, where all hatchlings head in the right direction into the sea (Tereza Znachorová, 2022).

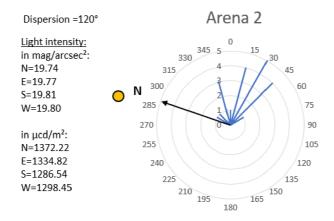


Figure 17. Arena located on an unlit part of the beach, where all hatchlings head in the right direction into the sea (Tereza Znachorová, 2022).

In arena 3 (Figure 18) and 4 (Figure 19) it is already evident that several turtles went the wrong way. The reason for this is approaching the illuminated part of the beach where the public lighting of Tortuguero town is located. The hatchlings were heading to the opposite side of the sea.

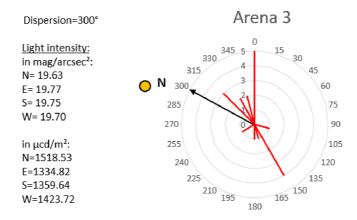


Figure 18. Area 3, where it is evident that the turtles are having trouble finding the sea and are heading in the wrong direction away from the sea (Tereza Znachorová, 2022).

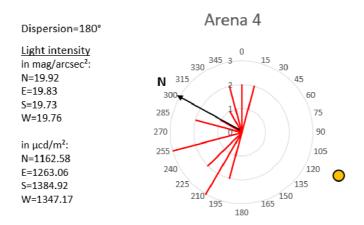


Figure 19. Area 4, where it is evident that the turtles are having trouble finding the sea and are heading in the wrong direction away from the sea (Tereza Znachorová, 2022).

At arena 5 (Figure 20), the turtles headed in the right direction again despite the fact that it was already in front of the town, meaning that the public lighting was covered by vegetation or a building and did not directly hit the beach. At arena 6 (Figure 21), most of the young went towards the sea with only 1 individual going in the opposite direction towards the town, which is the reason for the red colouration of the tracks.

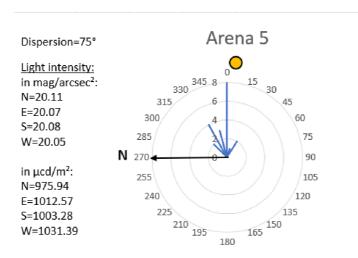


Figure 20. Arena located closer to the town, but yet all hatchlings head in the right direction into the sea (Tereza Znachorová, 2022).

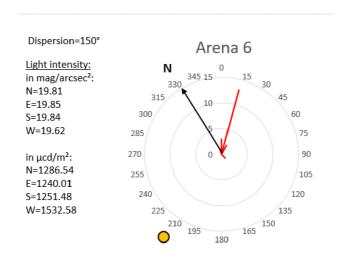


Figure 21. Arena located in front of the town, where most of the hatchlings head in the right direction into the sea, with only one individual going in the opposite way (Tereza Znachorová, 2022).

Most of the hatchlings from arenas 7 (Figure 22), 8 (Figure 23) and 9 (Figure 24) went in the right direction to the sea, only a few chose the wrong direction. A different situation occurs in arena 10 (Figure 25), 11 (Figure 26), 12 (Figure 27) and 13 (Figure 28) where a higher level of disorientation is evident, and a greater number of turtles chose the wrong direction to the bright artificial lighting.

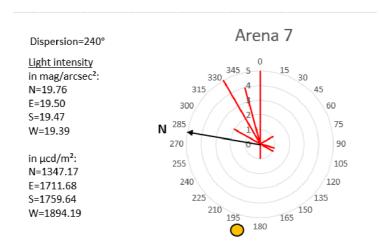


Figure 22. Arena, where most of the hatchlings headed in the right direction with only a few individuals choosing the direction away from the sea (Tereza Znachorová, 2022).

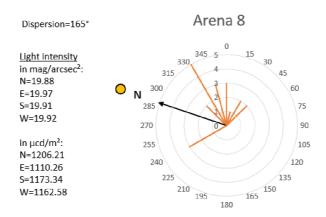


Figure 23. Arena, where most of the hatchlings headed in the right direction with only a few individuals choosing the direction away from the sea (Tereza Znachorová, 2022).

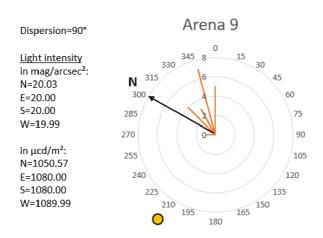


Figure 24. Arena, where most of the chicks headed in the right direction with only one individual choosing the direction away from the sea (Tereza Znachorová, 2022).

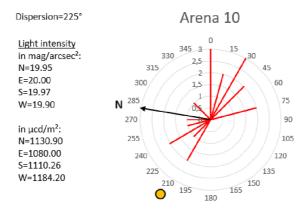


Figure 25. An arena showing a higher level of disorientation, where more hatchlings chose the wrong direction (Tereza Znachorová, 2022).

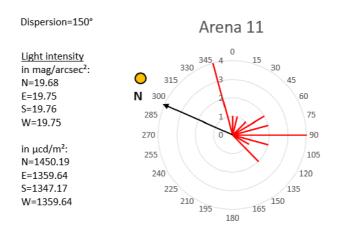


Figure 26. An arena showing a higher level of disorientation, where more hatchlings chose the wrong direction (Tereza Znachorová, 2022).

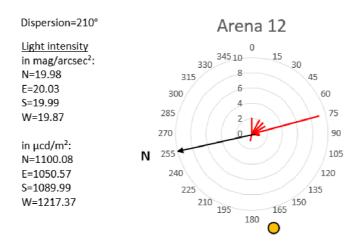


Figure 27. Arena, where most of the chicks went in the right direction, only a few chose the direction away from the sea (Tereza Znachorová, 2022).

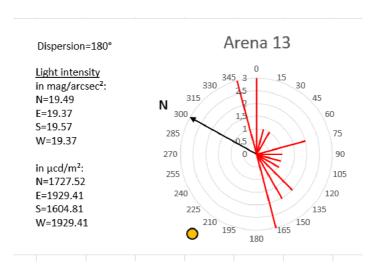


Figure 28. An arena showing a higher level of disorientation, where more hatchlings chose the wrong direction (Tereza Znachorová, 2022).

For arenas 14 (Figure 29), 15 (Figure 30) and 16 (Figure 31), disorientation is decreased because the arenas were again located in the unlit part of the study area, thus most of the juveniles are heading seaward. As we approached towards the illuminated city, the level of disorientation increased again, which is evident in arenas 17 (Figure 32), 18 (Figure 33), 19 (Figure 34), 20 (Figure 35) and 21 (Figure 36). In arena 22 (Figure 37), the hatchlings again chose the correct direction, and all headed towards the sea. This means that the artificial lighting was again blocked by vegetation as the arena was located in front of the town.

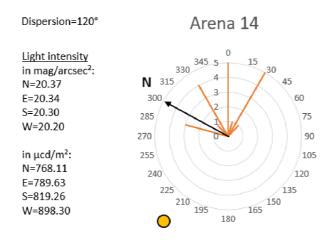


Figure 29. Arena, which was located on an unlit part of the beach and most of the hatchlings headed towards the sea (Tereza Znachorová, 2022).

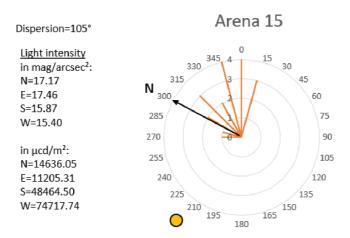


Figure 30. Arena, which was located on an unlit part of the beach and most of the hatchlings headed towards the sea (Tereza Znachorová, 2022).

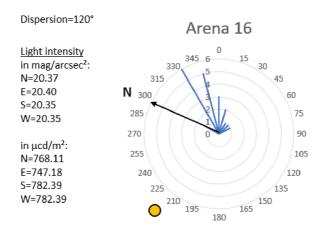


Figure 31. Arena, which was located on an unlit part of the beach and all hatchlings headed towards the sea (Tereza Znachorová, 2022).

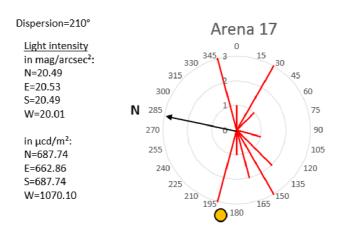


Figure 32. The arena located near the illuminated town, which again caused increased disorientation of the hatchlings (Tereza Znachorová, 2022).

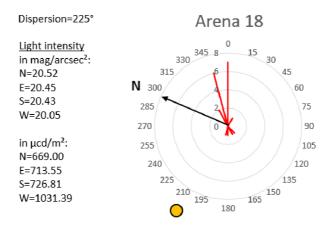


Figure 33. The arena located near the illuminated town, which again caused increased disorientation of some hatchlings (Tereza Znachorová, 2022).

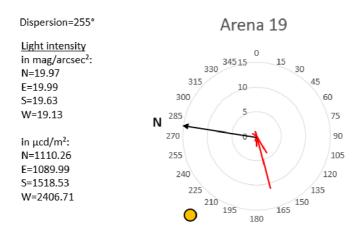


Figure 34. The arena located near the illuminated town, which again caused increased disorientation of the hatchlings (Tereza Znachorová, 2022).

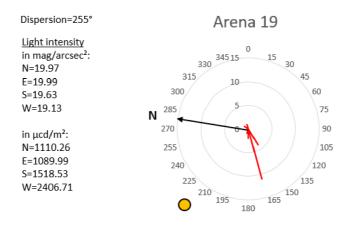


Figure 35. The arena located near the illuminated town, which again caused increased disorientation of the hatchlings (Tereza Znachorová, 2022).

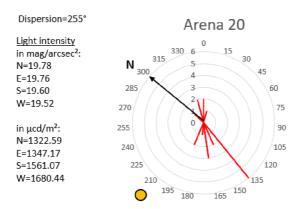


Figure 36. The arena located near the illuminated town, which again caused increased disorientation of the hatchlings (Tereza Znachorová, 2022).

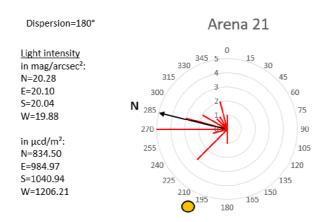


Figure 37. The arena located near the illuminated town, which again caused increased disorientation of the hatchlings (Tereza Znachorová, 2022).

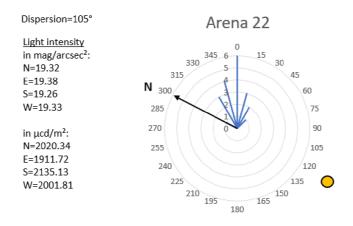


Figure 38. For this arena, disorientation is again great despite being in front of the city, which means the artificial light is shadowed by another object (Tereza Znachorová, 2022).

For the last 4 arenas, thus arenas 23 (Figure 39), 24 (Figure 40), 25 (Figure 41) and 26 (Figure 42), the full moon was present, which affected the whole orientation of the hatchlings as they still perceived the bright moonlight instead of the artificial illumination of the town.

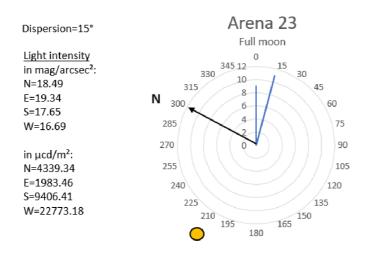


Figure 39. Arena in the presence of a full moon, when it is easiest for the cubs to go in the right direction (Tereza Znachorová, 2022).

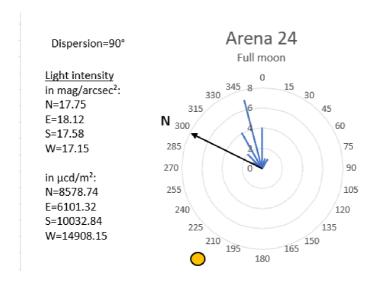


Figure 40. Arena in the presence of a full moon, when it is easiest for the cubs to go in the right direction (Tereza Znachorová, 2022).

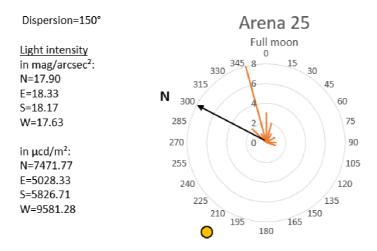


Figure 41. Arena in the presence of a full moon, when it is easiest for the cubs to go in the right direction (Tereza Znachorová, 2022).

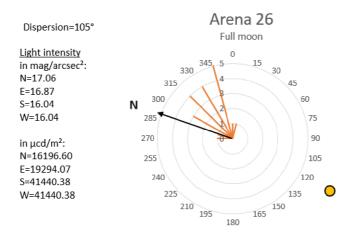


Figure 42. Arena in the presence of a full moon, when it is easiest for the cubs to go in the right direction (Tereza Znachorová, 2022).

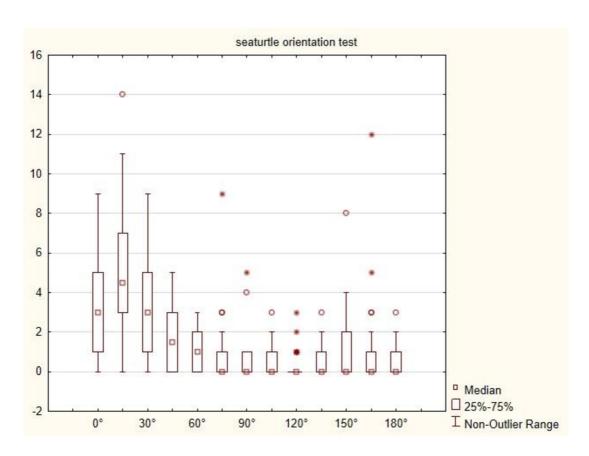


Figure 43. Box-plot showing the frequency of directions of hatching turtles to different sides.

Discussion

The results of my research were based on the topic of my thesis, the study focused on how artificial lighting affects the orientation of hatchling sea turtles. The research was conducted on a selected area of a nesting beach. The study area was chosen to be exposed to artificial lighting from a nearby town. This was determined by an observational method where hatchlings collected from wild and marked nests were released from several arenas in different locations in the study area. Turtles released in an area without artificial lighting had no problem finding the sea. The closer the arenas got to the illuminated area the worse the orientation of the hatchlings became. The time to leave the arena increased as the turtles could not decide which way to go. They headed out of the arenas in the wrong direction, moving in circles as they lost orientation completely, or went straight for the light. It was difficult for them to find the sea. In all test arenas, their movements were recorded, and data were collected. Analysis of these data established the results of the study. However, the results showed that artificial lighting from the town does have some effect on orientation, but only a small one. Most of the juveniles headed towards the sea despite the presence of artificial lighting. Only a minority followed the artificial light source. So, this fact contradicts my hypothesis. These findings are valid for this particular experiment, meaning for the species of green sea turtle, during the summer months of August and September, in Tortuguero, Costa Rica, during the rainy season. Despite this, I consider this study important for the future conservation of sea turtles.

These results also correspond to the current knowledge on the subject. Since sea turtle conservation is a studied topic, I was able to obtain enough material to compare my results with the conclusions of research studies by available authors. A similar topic was addressed by Witherington and Martin (2003), who focused on the different types of threats leading to the global decline of sea turtle populations. In addition to threats from fishing and interaction with marine debris, they focused on the effects of light smog on nesting turtles and hatchlings. The authors conducted their experiments on nesting beaches and studied how artificial lighting can affect hatchlings sea-finding ability. The experiments aimed to determine the degree of disorientation as one of the possible threats to life. The results authors showed that artificial lighting significantly

disrupts the orientation of hatchling sea turtles, and tens of thousands of hatchlings will die unnecessarily. Similar results were seen in a study by Salmon et al. (1995), and Kamrowski et al. (2015). Sea turtles rely on visual environmental cues for orientation, which potential artificial lighting will overlay and disrupt the natural nesting behaviour of turtles. Published results describe how nesting female sea turtles faced heavily lit coastal sites as well as unexpected construction when returning to their natal beaches. They preferred more secluded, dark beaches for nesting. The hatchlings were oriented by the bright light of the sea horizon, but unfortunately, these signals became less clear in the presence of artificial lighting. Again, these findings are consistent with the results of my study, which demonstrated impaired orientation by artificial lighting.

In relation to this topic, several authors have carried out an interesting study. Tuxbury and Salmon (2005), and Berry et al. (2013) focused on the intensity of visual light signals. They conducted their experiments on Florida nesting beaches. They investigated the response of sea turtles to light in different spectral ranges and wavelengths. Turns out the turtles are more attracted to the shorter wavelengths. To give an idea, these are blue, violet and ultraviolet light. In natural conditions, short-wavelength light is most intense towards the sea, allowing hatchlings to find the water. After hatching from the nest, they crawl quickly towards the ocean and orient themselves by visual light signals on the sea surface. However, when artificial lighting was nearby, the experiment showed a clear orientation of the hatchlings towards this light source. The artificial lighting also showed signs of shorter wavelengths and therefore disorientation of the juveniles. In contrast to my study, the researchers focused on the analysis of the intensity of the light sources, supporting our identical results. Artificial lighting has a similar wavelength to the illuminated marine horizon, therefore, in both cases, there was evidence of juvenile disorientation.

Similar conclusions were reached by Lorne & Salmon (2007) whose results showed that short-wavelength light significantly disrupts the perception of natural signals in hatchling turtles. Hatchlings are oriented towards artificial lighting, reducing their ability to find the ocean. Some hatchlings lost their orientation completely and moved in circles. This increased the likelihood of death due to exhaustion, dehydration or predation. Berry et al. (2013) experimented with hatchlings in the presence of artificial lighting. The conclusion of their experiment showed that the hatchlings

wandered for extended periods on the beach and crawled in search of artificial light. Some changed direction and exhibited circling behaviour. Their orientation was severely disturbed. By staying longer on the beach, the young were more at risk of death and mortality rates were higher. There is general agreement among all the authors cited. Artificial lighting disrupts the orientation of hatchlings. My study also showed severe disorientation and moving in circles, my results can be described as consistent with those of the authors.

Further evidence of the harmfulness of artificial lighting was provided by Harewood and Horrocks (2008). They observed juveniles that found the sea despite exposure to artificial lighting. The result of the experiment showed that disturbed orientation by exposure to artificial lighting affected the behaviour of hatchlings after reaching the sea. Even when the young finally found the sea, they were tired and much slower. Wandering on the beach consumed some of the energy that was missing during the demanding swim in the sea. The slow swimming speed made the hatchlings easier prey for predators in coastal waters. Although I did not observe the juveniles in the water anymore and my study did not include an analysis of mortality after reaching sea level, the authors' results and mine can be in agreement. For there is a greater threat of predation after reaching the sea for juveniles disoriented by artificial lighting.

During my study on the beach at Tortuguero, I noticed the possible influence of buildings and growing vegetation on beach shading. Where the nesting beach was shaded by mature trees and shrubs, the orientation of the hatchlings was not so disturbed. A similar issue was described by Witherington et al. (1990). They described how the intensity of artificial lighting can be influenced by the style of development, the vegetation growing or the season. Enclosing private properties with walls or lush vegetation can act as a light barrier. Artificial beach lighting may be different at various times and seasons. Tourist season, occupancy of buildings, or simply leaving lights on in garages and front of houses can have an impact. Also, a nearby highway or another road may influence animal behaviour by the lights of passing cars. Female sea turtles will nest depending on the conditions of the moment, this situation can occur after midnight when most people have their lights off. Hatchlings can hatch when the lights are on again. According to the authors of the study, most hatchlings emerge between dusk and midnight. Their ability to find the sea varied by location, with disorientation

greater in areas with little or no vegetation cover. Misorientation was also caused by differences in horizon height. The horizon is used by juveniles as a localization of the sea. Similar findings were previously published by van Rhijn and van Gorkum (1983). They investigated how juveniles respond to natural and urban silhouettes. The results showed that hatchlings perceive both horizontal height differences and vertical contours of objects. Similarly, in my study, vegetation shading light had a positive effect on the orientation of the hatchlings. They also managed the journey to the sea better if they were not blocked by horizontal or vertical barriers in the form of sand dunes, etc. The juveniles oriented best to the illuminated sea horizon without overcoming obstacles.

To conclude the discussion, I would like to answer the objectives of my thesis. The main objective was to analyse the effect of public lighting in the town of Tortuguero on the ability, of hatchling sea turtles to find the sea. The results of my research clearly showed that hatchlings are affected by artificial lighting originating from the urban area. Their orientation was disrupted or completely disoriented. They found it difficult or impossible to find the sea near public lighting. Their mortality rate increased significantly. The artificial lighting disrupted the orientation of the juveniles in two ways: the juveniles may crawl towards the lights, this is a misorientation. Or they cannot crawl in any direction and show circular movements, this is disorientation. These results are consistent with the research results of the cited authors.

Therefore, the hypothesis that the success rate of finding the sea in hatchling sea turtles is reduced in the case of artificial lighting has also been tested and confirmed.

5. Conclusions

Based on the study performed, the thesis found that artificial lighting influenced the behaviour of hatchling sea turtles. Their orientation was significantly disturbed or completely disoriented. They were moving in the wrong direction as they made their way to the sea, choosing the path towards artificial light instead of the natural light reflecting off the sea horizon. Some juveniles lost orientation completely and moved in circles in confusion. They were so disoriented that they chose no direction. The artificial lighting affected their ability to find the sea and increased the likelihood of death. Reasons for the higher mortality of disoriented juveniles were exhaustion, dehydration or death due to predators.

The results of the study clearly showed that as the intensity of artificial lighting increased, the disorientation of hatchlings became greater. The further away from the urban illuminated development, the better they were able to find the sea surface. The closer the experimental arenas were to the artificially lit urban development, the more disoriented the hatchlings became.

From the results of my thesis, certain recommendations emerged that could lead to conservation activities in coastal nesting beach areas. This would be a significant help in protecting sea turtles as an endangered species. Targeted shading of artificial lighting would be a solution. One option would be to plant lush vegetation to prevent light from reaching the beach. Also, the construction of walls along the development with artificial lighting would greatly help. Since turtles are attracted to shorter wavelength light, replacing artificial lighting with higher wavelength lights, so-called sea turtle-friendly lights, could be very important. This thesis serves as a baseline for further studies dealing with this issue, which can be further developed and improved. Specifically, for STC, which intends to repeat the research after the replacement of public lighting.

Research and studies leading to the conservation of sea turtles should continue to be developed and improved. The findings could significantly help to stop the decline in the population curve of the most endangered species.

6. References

Ackerman RA. 1997. The nest environment and the embryonic development of sea turtles. Pages 83-106 in Lutz PL and Musick JA editors. The Biology of Sea turtles. CRC Press, Boca Raton.

Amorocho DF, Reina RD. 2007. Feeding ecology of the East Pacific green sea turtle Chelonia mydas agassizii at Gorgona National Park, Colombia. Endangered Species Research **3:** 43–51.

Arulmoorthy MP, Srinivasan M. 2019. Sea Turtles. Environmental information system resource partner, India.

Arthur KE, Boyle MC, Limpus CJ. 2008. Ontogenetic changes in diet and habitat use in green sea turtles (*Chelonia mydas*) life history. Marine Ecology Progress Series **362**: 303–311.

Arthur KR, O'Niel JM, Limpus CJ, Abernathy K, Marshall G. 2007. Using animal-bourne imaging to assess green turtle (Chelonia mydas) foraging ecology in Moreton Bay, Australia. Marine Technology Society Journal **41:** 9–13.

Bartol SM, Musick JA. 2002. Visual acuity thresholds of juvenile loggerhead sea turtles (*Caretta caretta*): an electrophysiological approach.

Berkson H. 1967. Physiological adjustments to deep diving in the Pacific green turtle (*Chelonia mydas agassizii*). Comparative Biochemistry and Physiology **21**: 507–524.

Berry M, Booth DT, Limpus CJ. 2013. Artificial lighting and disrupted sea-finding behaviour in hatchling loggerhead turtles (Caretta caretta) on the Woongarra coast, south-east Queensland, Australia. Australian journal of zoology **2:** 137-145.

Berube MD, Dunbar SG, Rützler K, Hayes WK. 2012. Home range and foraging ecology of juvenile hawksbill turtles (*Eretmochelys imbricata*) on inshore reefs of Honduras. Chelonian Conservation and Biology **11:** 33–43.

Bieser KL, Wibbels T, Mourad G, Paladino F. 2013. The cloning and expression analysis of Lhx9 during gonadal sex differentiation in the red-eared slider turtle, Trachemys scripta, a species with temperature-dependant sex determination. Journal of Experimental Zoology B **320**: 238–246.

Bird BL, Branch LC, Miller DL. 2004. Effects of coastal lighting on foraging behaviour of beach mice. Conservation Biology **18:** 1435-1439.

Bjorndal KA, Bolten A, Chaloupka MY. 2000. Green turtle somatic growth model: evidence for density dependence. Ecological Applications **10**: 269-282.

Booth DT, Evans A. 2011. Warm water and cool nests are best. How global warming might influence hatchling green turtle swimming performance. PLOS ONE.

Bradshaw CJA, McMahon CR, Hays GC. 2007. Behavioral inference of diving metabolic rate in free-ranging leatherback turtles. Physiological and Biochemical Zoology **80**: 209–219.

Brothers JR, Lohmann KJ. 2018. Evidence that magnetic navigation and geomagnetic imprinting shape spatial genetic variation in sea turtles. Current Biology **28**: 1325–1329.

Brudenall DK, Schwab IR, Fritsches KA. 2008. Ocular morphology of the Leatherback sea turtle (*Dermochelys coriacea*). Veterinary ophthalmology **2:** 99-110.

Clarke GL, Denton EJ. 1962. Light and animal life. Pages 456-468 in Hill MN editor. In The Sea. London.

Constant N. 2015. Geospatial assessment of artificial lighting impacts on sea turtles in Tortuguero, Costa Rica [MSc. Thesis]. Nicholas School of the Environment of Duke University, Durham.

Davenport J, Fraher J, Fitzgerald E, McLaughlin P, Doyle T, Harman L, Cuffe T, Dockery P. 2009. Ontogenetic changes in tracheal structure facilitate deep dives and cold water foraging in adult leatherback sea turtles. The Journal of Experimental Biology **212**: 3440–3447.

Doyle TK, Houghton JDR, O'Su'illeabha'in F, Hobson VJ, Marnell F, Davenport J, Hays GC. 2008. Leatherback turtles satellite-tracked in European waters. Endangered Species Research 4: 23–31.

Duchene S, Frey A, Alfaro-Nu'n ez A, Dutton PH, Gilbert MPG, Morin PA. 2012. Marine turtle mitogenome phylogenetics and evolution. Molecular Phylogenetics and Evolution **65**: 241–250.

Ferrera CR, Vogt RC, Sousa-Lima RS. 2013. Turtle vocalization as the first evidence of posthatching parental care in chelonians. Journal of Comparative Psychology **127**: 24–32.

Gaos, AR, Abreu-Grobois FA, Alfaro-Shigueto J, Amorocho D, Arauz R, Baquero A, Briseño R, Chacón D, Dueñas C, Hasbún C, Liles M, Mariona M, Muccio C, Muñoz JP, Nichols WJ, Peña M, Seminoff JA, Vásquez M, Urteaga J, Wallace BP, Yañez I, Zárate P. 2010. Signs of hope in the eastern Pacific: international collaboration reveals encouraging status for severely depleted population of hawksbill turtles. Oryx **44**: 595–601.

Gaston KJ, Davies TW, Bennie J, Hopkins J. 2012. Reducing the ecological consequences of night-time light pollution: options and developments. Journal of Applied Ecology **49:** 1256-1266.

Godley BJ, Broderick AC, Frauenstein R, Glen F, Hays GC. 2002. Reproductive seasonality and sexual dimorphism in green turtles. Marine Ecology Progress Series **226**: 125-133.

Gutiérrez-Lince J, Palacios MD, Valverde RA. 2021. Case Study: The Evolution of Tourism and Sea Turtle Conservation at Tortuguero National Park, Costa Rica. In Sea Turtle Research and Conservation. Academic Press 105-111.

Harewood A, Horrocks J. 2008. Impacts of coastal development on hawksbill hatchling survival and swimming success during the initial offshore migration. Biological Conservation **2:** 394-401.

Hart KM, Zawada DG, Fujisaki I, Lidz, BH. 2010. Inter-nesting habitat-use patterns of loggerhead sea turtles: Enhancing satellite tracking with benthic mapping. Aquatic Biology **11:** 77–90.

Hatase H, Omuta K, Tsukamoto K. 2007. Bottom or midwater: Alternative foraging behaviours in adult female loggerhead sea turtles. Journal of Zoology **273**: 46–55.

Hailman, JP, Elowson AM. 1992. Ethogram of the nesting female loggerhead (*Caretta caretta*). Herpetologica **48:** 1–30.

Hays GC, Fossette S, Katselidis KA, Schofield G, Gravenor MB. 2010. Breeding periodicity for male sea turtles, operation sex ratios, and implications in the face of climate change. Conservation Biology **24**: 1636–1643.

Hendrickson JR. 1958. The green sea turtle, *Chelonia mydas* in Malaya and Sarawak. In Proceedings of the Zoological Society of London **13:** 455-535.

Hendrickson JR. 1995. Nesting behaviour of sea turtles with emphasis on physical and behavioural determinants of nesting success or failure. Pages 53-57 in Bjorndal KA editors. Biology and Conservation of Sea Turtles, Revised Edition. Washington, D.C.: Smithsonian Institution Press.

Hirth HF. 1997. Synopsis of the biological data on the green turtle *Chelonia mydas*. Biological Report 97(1), Fish and Wildlife Service, U.S. Dept of the Interior. 120 pp.

Hochscheid S, Bentivegna F, Hays GC. 2005. First dive durations for a hibernating sea turtle. Biology Letters 1: 82–86.

Horvát G, Varjú D. 2004. Polarized Light in Animal Vision: Polarization Pattern in Nature. Germany: Springer Verlag.

Howland HC, Merola S, Basarab JR. 2004. The allometry and scaling of the size of the vertebrate eye. Vision Research 44: 2043-2065.

Hölker F, Moss T, Griefahn B, Kloas W, Voigt CC, Henckel D, Tockner K. 2010. The dark side of light: a transdisciplinary research agenda for light pollution policy. Ecology and Society **15**: 13.

Hu Z, Hu H, Huang Y. 2018. Association between nighttime artificial light pollution and sea turtle nest density along Florida coast: A geospatial study using VIIRS remote sensing data. Environmental Pollution **239**: 30-42.

Hudson DM, Lutz PL. 1986. Salt gland function in the leatherback sea turtle. *Dermochelys coriacea*. Copeia 1: 247-249.

Humber F, Godley BJ, Ramahery V, Broderick AC. 2011. Using community members to assess artisanal fisheries: The marine turtle fishery in Madagascar. Animal Conservation **14:** 175–185.

Chaloupka M. 2001. Historical trends, seasonality and spatial synchrony in green sea turtle egg production. Biological Conservation **101**: 263–279.

Chaloupka MY, Musick JA. 1997. Age, growth, and population dynamics. Pages 233-276 in Lutz PL and Musick JA editors. The Biology of sea turtles I. Boca Raton, FL: CRC Press.

Irwin WP, Lohmann KJ. 2005. Disruption of magnetic orientation in hatchling loggerhead sea turtles by pulsed magnetic fields. Journal of Comparative Physiology. A **191:** 475–480.

Jagger WS, Muntz WRA. 1993. Aquatic vision and the modulation transfer properties of unlighted and diffusely lighted natural waters. Vision Research **33**: 1755-1763.

Johnsen S. 2006. Mathematical model of the visual abilities of sea turtles and pelagic fishes. Sea turtle and pelagic fish sensory biology: developing techniques to reduce sea turtle bycatch in longline fisheries 18-23.

Jong G, deHave TMVD, Whitman DW, Ananthakrishnan TN. 2009. Temperature dependence of development rate, growth rate and size: From biophysics to adaptation. Pages 523-588 in Whitman DW and Anantha-Krishnan TN editors. Phenotypic plasticity of insects: Mechanisms and consequences. Science Publishers.

Jones TM, Durrant J, Michaelides EB, Green MP. 2015. Melatonin: a possible link between the presence of artificial light at night and reductions in biological fitness. Philos.

Kamrowski RL, Limpus C, Pendoley K, Hamann M. 2015. Influence of industrial light pollution on the sea-finding behaviour of flatback turtle hatchlings. Wildlife Research **5:** 421-434.

Kear BP, Lee MSY. 2006. A primitive protostegid from Australia and early sea turtle evolution. Biology Letters 2: 116–119.

Levenson DH, Eckert SA, Crognale MA, Deegan IIJF, Jacobs GH. 2004. Photopic spectral sensitivity of Green and loggerhead Sea Turtles. Copeia 4: 908-914.

Limpus CJ. 1971. The flatback turtle, *Chelonia depressa* Garman in southeast Queensland, Australia. Herpetologica 431-446.

Limpus C, Kamrowski RL. 2013. Ocean-finding in marine turtles: the importance of low horizon elevation as an orientation cue. Behaviour **8**: 863-893.

Lohmann KJ, Putman NF, Lohmann CMF. 2008. Geomagnetic imprinting: A unifying hypothesis of long-distance natal homing in salmon and sea turtles. Proceedings of the National Academy of Sciences of the USA **105**: 19096–19101.

Lohmann KJ, Witherington BE, Lohmann CM, Salmon M. 1997. Orientation, navigation, and natal beach homing in sea turtles. In The biology of sea turtles. CRC Press.

Longcore T, Rich C. 2004. Ecological light pollution. Frontiers in Ecology and the Environment 2: 191-198.

Lorne J, Salmon M. 2007. Effects of exposure to artificial lighting on orientation of hatchling sea turtles on the beach and in the ocean. Endang Species Res. 3: 23-30.

Lutcavage ME, Bushnell PG, Jones DR. 1990. Oxygen transport in the leatherback sea turtle Dermochelys coriacea. Physiological Zoology **63**: 1012–1024.

Lutz PL, Musick JA, Wyneken J. 2002. The biology of sea turtles, Volume II. CRC press.

Lyson TR, Bever GD, Bhullar B-A, Joyce WG, Gauthier JA. 2010. Transitional fossils and the origin of turtles. Biology Letters **6**: 830–833.

Mäthger LM, Litherland L, Fritsches KA. 2007. An anatomical study of the visual capabilities of the green turtle, Chelonia mydas. Copeia, **1:** 169-179.

Meletis ZA. 2007. Wasted Visits? Ecotourism in Theory vs. Practice, at Tortuguero, Costa Rica [Ph.D. Thesis]. Duke University, Durham.

Miller JD. 1997. Reproduction in sea turtles. Pages 51-58 in Lutz PL and Musick JA editosr. The Biology of Sea Turtles, Vol. I. CRC Press, Boca Raton.

Musick JA, Limpus CJ. 1997. Habitat utilization and migration in juvenile sea turtles. Pages 137-163 in Lutz PL, Musick JA, editors. The Biology of Sea Turtles, Vol. I. CRC Press, Boca Raton.

Neeman N, Harrison E, Wehrtmann IS, Bolaños F. 2015. Nest site selection by individual leatherback turtles (*Dermochelys coriacea*, Testudines: Dermochelyidae) in Tortuguero, Caribbean coast of Costa Rica. Revista de Biologia Tropical **2**: 491-500.

Nichols WJ, Resendiz A, Seminoff JA, Beatrice R. 2000. Transpacific migration of a loggerhead turtle monitored by satellite telemetry. Bulletin of Marine Science **67:** 937–947.

Northmore DPM, Granda AM. 1991. Ocular dimensions and schematic eyes of freshwater and sea turtles. Visual neuroscience **6**: 627-635.

Paladino FV, O'Connor MP, Spotila JR. 1990. Metabolism of leatherback turtles: gigantothermy and thermoregulation of dinosaurs. Nature **344**: 858–860.

Paladino FV, Robinson NJ. 2013. Sea Turtles. Earth Systems and Environmental Sciences. Elsevier.

Phillips KP, Jorgensen TH, Jolliffe KG, Jolliffe S-M, Henwood J, Richardson DS. 2013. Reconstructing paternal genotypes to infer patterns of sperm storage and sexual selection in the hawksbill turtle. Molecular Ecology **22**: 2301–2312.

Pilcher NJ, Enderby S, Stringell T, Bateman L. 2000. Nearshore turtle hatchling distribution and predation in Sabah, Malaysia. Pages 27-29 in Kalb H, Wibbels T editors. Proceedings of the 19th Annual Sea Turtle Symposium, vol. 443.

Place S. 1988. The impact of national park development on Tortuguero, Costa Rica. Journal of Cultural Geography 9: 37-52.

Plotkin P. 2003. Adult habitat use and migrations. Pages 225–241 in Lutz PL, Musick JA, Wyneken J, editors. The Biology of Sea Turtles, Vol. 2. CRC Press, Boca Raton.

Polovina JJ, Howell E, Parker DM, Balazs GH. 2003. Dive-depth distribution of loggerhead (*Carretta carretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: Might deep longlines sets catch fewer turtles? Fisheries Bulletin **101**: 189–193.

Price ER, Wallace BP, Reina RD, Spotila JR, Paladino FV, Piedra R, Ve'lez E. 2004. Size, growth, and reproductive output of adult female leatherback turtles Dermochelys coriacea. Endangered Species Research 1: 41–48.

Putman NF, Bane JM, Lohmann KJ. 2010. Sea turtle nesting distributions and oceanographic constraints on hatchling migration. Proceedings of the Royal Society B Biological Sciences **277**: 3631–3637.

Reina RD, Jones TT, Spotila JR. 2002. Salt and water regulation by the leatherback sea turtle Dermochelys coriacea. The Journal of Experimental Biology **205**: 1853–1860.

Renous S, Bels V, Davenport J. 2000. Locomotion in marine Chelonia: Adaptation to the aquatic habitat. Historical Biology **14:** 1–13.

Rusli MU. 2019. Nesting of Sea Turtles. Encyclopedia of animal cognition and behavior. Springer International Publishing. Malaysia.

Saba VS, Stock CA, Spotila JR, Paladino FV, Santidria'n Tomillo P. 2012. Projected response of an endangered marine turtle population to climate change. Nature Climate Change **2:** 814–820.

Sale A, Luschi P, Mencacci R, Lambardi P, Hughes GR, Hays GC, Benvenuti S, Papi F. 2006. Long-term monitoring of leatherback turtle diving behaviour during oceanic movements. Journal of Experimental Marine Biology and Ecology **328**: 197–210.

Salmon M, Witherington BE. 1995. Artificial lighting and seafinding by loggerhead hatchlings: evidence for lunar modulation. Copeia 931-938.

Salmon M, Witherington BE, Elvidge CD. 2000. Artificial lighting and the recovery of sea turtles. Pages 25-34 in Pilcher N, Ismail G editors. Sea Turtles of the Indo-Pacific: Research, Management and Conservation. ASEAN Academic Press, London.

Salmon M, Wyneken J, Fritz E, Lucas M. 1992. Seafinding by hatchling sea turtles: role of brightness, silhouette and beach slope as orientation cues. Behaviour 1: 56-77.

Segura LN, Cajade R. 2010. The effects of sand temperature on pre-emergent green sea turtle hatchlings. Herpetological Conservation and Biology **5**: 196–206

Shigenaka G, Stacy BA, Wallace BP. 2021. Oil and Sea Turtles BIOLOGY, PLANNING, AND RESPONSE. National Oceanic and Atmospheric Administration.

Shillinger GL, Palacios DM, Bailey H, Bograd SJ, Swithenbank AM, Gaspar P, Wallace BP, Spotila JR, Paladino FV, Piedra R, Eckert SA, Block BA. 2008. Persistent leatherback turtle migrations present opportunities for conservation. PLoS Biology 6: e171.

Schmid JR. 1998. Marine turtle populations on the west central coast of Florida: results of tagging studies at the Cedar Keys, Florida. Fisheries Bulletin **96**: 589-602.

Sims M, Bjorkland R, Mason P, Crowder LB. 2008. Statistical power and sea turtle nesting beach surveys: How long and when? Biological Conservation **141**: 2921–2931.

Spotila JR, Reina RD, Steyermark AC, Plotkin PT, Paladino FV. 2000. Pacific leatherback turtles face extinction. Nature **405**: 529–530.

Talbert OR, Stancyk SE, Dean JM, Will JM. 1980. Nesting activity of the loggerhead turtle (*Caretta caretta*) in South Carolina I: A rookery in transition. Copeia 709–719.

Tröeng S, Ranking E. 2005. Long-term conservation efforts contribute to positive green turtle Chelonia mydas nesting trend at Tortuguero, Costa Rica, Biological Conservation **121**: 111-116.

Tuxbury SM, Salmon M. 2005. Competitive interactions between artificial lighting and natural cues during seafinding by hatchling marine turtles. Biological Conservation **121**: 311–316.

Valverde RA, Wingard S, Go'mez F, Tordoir MT, Orrego CM. 2010. Field lethal incubation temperature of olive ridley sea turtle Lepidochelys olivacea embryos at a mass nesting rookery. Endangered Species Research **12**: 77–86.

Van Rhijn, FA., Van Gorkom JC. 1983. Optic orientation in hatchlings of the sea turtle, *Chelonia mydas*. III. Sea-finding behaviour: The role of photic and visual orientation in animals walking on the spot under laboratory conditions. Marine & Freshwater Behaviour & Phy 3: 211-228.

Wallace BP, Kilham SS, Paladino FV, Spotila JR. 2005. Energy budget calculations indicate resource limitation in Eastern Pacific leatherback turtles. Marine Ecology Progress Series **318**: 263–270.

Wallace BP, Lewison RL, McDonald SL, McDonald RK. 2010. Global patterns of marine turtle bycatch. Conservation Letters **3**: 131-142

Walker TA, Parmenter CJ. 1990. Absence of pelagic phase in the life cycle of flatback turtle, *Natator depressa*. Journal of Biogeography **17**: 275-278.

Warrant EJ, Locket NA. 2004. Vision in the deep sea. Biological Reviews 3: 671-712.

Witherington BE. 1992. Behavioral responses of nesting sea turtles to artificial lighting. Herpetologica **48**: 31-39

Witherington BE, Bjorndal KA, McCabe CM. 1990. Temporal pattern of nocturnal emergence of loggerhead turtle hatchlings from natural nests **4:** 1165-1168.

Witherington BE, Bresette M, Herren R. 2006. Chelonia mydas—green turtle. Biology and Conservation of Florida Turtles. Chelonian Research Monographs 3: 90-104.

Witherington BE, Martin RE. 2003. Understanding, Assessing, and Resolving Light Pollution Problems on Sea Turtle Nesting Beaches. Florida Marine Research Institute, St. Petersburg, Florida.

Wyneken J. 2001. The Anatomy of Sea Turtles. U.S. Department of Commerce NOAA Technical Memorandum NMFS-SEFSC-470, 1-172 pp.

Wyneken J, Lohmann KJ, Musick JA. 2013. The biology of sea turtles (Vol. 3). CRC press. Florida.

Wyneken J, Salmon M. 1992. Frenzy and post frenzy swimming activity in loggerhead, green, and leatherback hatchling sea turtles. Copeia 478–484.

Appendices

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Appendix 1: Appendix title